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Energy and Nutrient Dynamics of Spider and Orthopteran Populations in a Grassland Ecosystem

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ENERGY AND NUTRIENT DYNAMICS OF SPIDER AND ORTHOPTERAN POPULATIONS IN A GRASSLAND ECOSYSTEM[1]

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ABSTRACT

Population dynamics, energy budgets, and nutrient concentrations were used to develop a compartment model for evaluating energy flow and nutrient fluxes in the spider and orthopteran components of an eastern Tennessee grassland ecosystem. The arthropod community consisted of: herbivores—*Melanoplus sanguinipes* (Acrididae), *Conocephalus fasciatus* (Tettigoniidae), and several of the Homoptera-Hemiptera; omnivore—*Pteronemobius fasciatus* (Gryllidae); and predators—*Lycosa* spp. (Lycosidae). Weekly estimates of arthropod density and biomass and monthly estimates of vegetation biomass were made during the 1968–69 growing season. Supporting studies included: (1) determination of caloric equivalents; (2) measurements of arthropod metabolism; (3) determination of whole-body concentrations of Na, Ca, and K; (4) estimation of biological turnover rates of these nutrients with radioactive analogues; and (5) field studies of arthropod feeding habits and food consumption.

Total net primary production of the grassland ecosystem was 1,274 kcal/m^2; 89% of this total was by grass species (*Festuca arundinacea* and *Andropogon virginicus*) and 11% by green forbs. Herbivores and omnivores consumed 9.6% (122.9 kcal/m^2) of net primary production. Annual net secondary production by the insect community was 32.05 kcal/m^2. Total net tertiary production by spiders was 2.26 kcal/m^2. Total annual energy flow (= total assimilation) through the community was 75.6 kcal/m^2. Herbivores accounted for 79.8% of this total, omnivores 12.2%, and predators 8.1%.

Whole-body concentrations of sodium increased with higher trophic position in the food chain: vegetation (0.43 mg/g ash free dry wt = AFDW), prey (1.18 mg/g AFDW), and predators (1.94 mg/g AFDW). Calcium concentrations decreased from vegetation (5.82 mg/g AFDW) to prey (0.85 mg/g AFDW) and remained constant to predators (0.88 mg/g AFDW). Potassium concentrations were much higher in vegetation (14.28 mg/g AFDW) than in either the prey (1.87 mg/g AFDW) or predators (1.96 mg/g AFDW), which were essentially the same. Sodium and potassium behaved similarly in their movement through arthropod food chains. The low concentrations of calcium in arthropod trophic levels and the rapid elimination

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of this element from each trophic level suggest that calcium is not as limiting as are sodium and potassium in this arthropod community.

Herbivores, the dominant members of the arthropod fauna, attained a maximum standing crop of 927 mg/m^2 (*Melanoplus* = 705 mg/m^2, *Conocephalus* = 200 mg/m^2, and the Homoptera-Hemiptera = 22 mg/m^2). This trophic level was responsible for 85% of the sodium turnover, 76% of the calcium turnover, and 78% of the potassium turnover by the arthropod component of the ecosystem. The omnivore *Pteronemobius* fed equally well on fresh vegetation and on litter. It reached a maximum biomass of 194 mg/m^2 and utilized 10% of the sodium, 22% of the calcium, and 20% of the potassium which passed through the arthropod community. The predator (*Lycosa* spp.) biomass reached a maximum of 146 mg/m^2 in late fall and was responsible for 5% of the sodium, 2% of the calcium, and 2% of the potassium utilized by the arthropod component of the ecosystem. Wolf spiders consumed 21% of total net secondary production. Absence of other predator species in collections from the arthropod community suggests that *Lycosa* was the dominant invertebrate predator in this grassland ecosystem.

INTRODUCTION

Secondary producers interact within the ecosystem as consumers, utilizing and recycling the products of net primary production. Thus, animals occupy a basic functional role, contributing to and affecting the integrity of the system.

Numerically, arthropods generally dominate the animal populations of natural ecosystems. Only recently, however, have ecologists begun to consider the functional role of the arthropod component of communities within terrestrial ecosystems. Relatively few studies have considered the regulatory mechanisms within these communities which affect population structure and size. All entomophagous arthropods (e.g., spiders) are secondary consumers and may contribute significantly in maintaining community homeostasis. Menhinick (1967) reported that spiders constitute over 50% of both numbers and biomass of carnivorous arthropods. Breymeyer (1967) found that the wandering spiders (principally lycosids) were important predators in meadows. Itô, Miyeshita, and Sekiguchi (1962) have studied the effects of spider populations on rice crop insect pests. A number of studies have investigated the occurrence (Barns 1953), numbers (Barns and Barns 1955), and niche relationships (Kuenzler 1958) of grassland spider populations. No studies on spider populations, however, have attempted to assess all of the following: (1) their role in regulating prey population numbers; (2) their contribution to the total standing crop of the arthropod community; and (3) their function in energy flow and nutrient transfers in ecosystems.

The primary objective of the present study was to investigate the flux of energy and nutrient resources (sodium, calcium, and potassium) through a three-trophic-level (plant to herbivore to predator) system in a grassland ecosystem. The specific objectives of the study were: (1) to determine the standing crops of biomass, energy, and selected nutrients on a seasonal basis for selected species at each trophic level; 2) to determine the annual net production in each trophic level; 3) to investigate the distribution and transfer rates of selected radionuclides through arthropod food chains when introduced into living vegetation; 4) to investigate the functional role of lycosid spider populations in terms of energy flow and nutrient transfers; and 5) to construct a compartmental model to mathematically depict trophic dynamics in a seasonal context.

METHODS AND MATERIALS

The study area

The study area was an old field located on the U. S. Atomic Energy Commission Reservation (Oak Ridge National Laboratory) in Roane County, Tennessee. The field, approximately 40 acres, was characterized by the codominance of Kentucky-31 fescue (*Festuca arundinacea* Schreb.) and broomsedge (*Andropogon virginicus* L.). The low, poorly drained areas of the field were dominated by the genera *Juncus* and *Diodia*; the upland areas contained *Rubus, Daucus, Plantago,* and *Solidago* in addition to the two dominant grasses. A floristic checklist of plant species collected from the area during this study may be found in Van Hook (1970).

The area was in agricultural use prior to 1942 and was planted in loblolly pine (*Pinus taeda* L.) in 1956 after lying fallow for 14 years. In 1964 the pines were removed and the area was planted in *Festuca*. Except for an occasional mowing prior to 1967, the area received no further treatment. The geology, soils, vegetation, and climate have been described in detail by Kelly et al. (1969). The climate of this part of eastern Tennessee is typically humid and mesothermal; the mean annual rainfall is 124 cm and the mean annual temperature, 14.9°C. Total annual rainfall during the 1968–69 growing season was 101 cm. The mean annual temperature during this period was 14.0°C.

Sampling procedures

Vegetation.—Plant biomass was determined by sampling the vegetation at 6-week intervals for 1 year on twelve 0.25-m^2 quadrats at six randomly determined locations. The litter was collected prior to

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clipping each sample. After the vegetation was harvested, it was sorted into four categories: living grass leaves, standing dead grass leaves, grass litter, and forbs. The samples were then ovendried at 105°C for 24 hr, weighed to the nearest 0.1 g, and stored for further processing.

Arthropods.—Insects and spiders were sampled weekly from April through December by a modified version of the "quick trap" method described by Turnbull and Nicholls (1966). Eight cylindrical cages, 0.25 m^2 by 1 m high, were placed in randomly selected locations at each sampling period during the early morning hours when arthropod activity was at a minimum. Later in the morning when the dew had evaporated, the cages were cleaned out with a vacuum insect collector (manufactured by the D-Vac Co., Riverside, California). The samples were sorted in the laboratory, identified, and stored in 80% ethanol. When all samples were collected, they were dried at 105°C for 24 hr, weighed to the nearest 0.01 mg, and stored in desiccators.

Radioisotope techniques

Three radioisotopes, ^{47}Ca, ^{42}K, and ^{22}Na, were utilized in determining the turnover rates of calcium, potassium, and sodium in the following arthropod species: *Melanoplus sanguinipes* G. and B. (grasshopper), *Conocephalus fasciatus* (De Geer) (grasshopper), *Pteronemobius fasciatus* (De Geer) (cricket), and *Lycosa punctulata* Hentz (wolf spider). Adults of these species were collected from the field site and allowed to become acclimated to experimental temperatures of 15°, 20°, and 25°C for 72 hr. The physical half-lives of the radioisotopes employed were: ^{47}Ca, 4.8 days; ^{42}K, 12.5 hr; and ^{22}Na, 2.5 years. A Packard auto-gamma spectrometer equipped with a 3- by 3-inch NaI(Tl-activated) well crystal was used for all counting. The counting efficiency was 19.6% for ^{47}Ca, 6.5% for ^{42}K, and 8.9% for ^{22}Na. All radioactivity measurements were corrected for decay by comparison with appropriate standards.

Separate experiments were conducted for each arthropod species on each radioisotope at all three experimental temperatures. In each experiment the insects were allowed to feed for 24 hr on fresh fescue shoots which had been placed in radioisotope solution for 24 hr. These shoots were positioned in containers so that only the lower 2 inches were immersed in the solution. The containers were then placed in a greenhouse so that uptake of radioisotope occurred by transpiration of the shoots. After 24 hr the lower portion of the shoot was removed and the remainder given to the insects. This procedure reduced the probability of external contamination of grasshoppers and crickets by radioactive material. All insects were maintained in cages fitted with wire bottoms which allowed fecal material to fall through, thereby preventing reingestion of radioisotopes. Spiders were tagged with radioisotopes by allowing them to feed on cricket nymphs (*Pteronemobius*) which had been tagged with fescue shoots. Cricket remains were removed from cages after spiders discarded them. All spiders were housed in individual cages. The radioactive food was removed from all cages after 24 hr of feeding and replaced with nontagged food; thereafter food and water were changed daily.

To determine the biological loss rates (k_b) of the radioisotopes, the radioactivity of the animal at the end of the 24-hr feeding period (tagged food) was determined and this value was taken as 100%. The decrease in radioactivity through time for each animal was then determined, and the value at each counting period was expressed as a percentage of the initial value. This procedure was continued until the activity remaining was approximately 5% of the initial value. The retention measurements (percentage) through time were used in a nonlinear regression analysis for calculating the effective elimination coefficients (λ_e). The calculations were determined with the following relationship:

$$A_t = A_o(a_1 e^{-\lambda_{e_1} t} + a_2 e^{-\lambda_{e_2} t}) \quad , \qquad (1)$$

where A_t is the activity at time t, A_o is the initial activity, a_1 is the nonassimilated fraction, a_2 is the assimilated fraction ($a_1 + a_2 = 1$), λ_{e_1} is the elimination coefficient associated with the nonassimilated fraction, and λ_{e_2} is the elimination coefficient associated with the assimilated fraction (Reichle and Crossley 1965). In cases where the assimilation of the radioisotope is complete ($a_1 = 0$), the first term in equation 1 becomes zero and the equation is then

$$A_t = A_o e^{-\lambda_e t} \quad , \qquad (2)$$

which describes a single component elimination curve. The biological elimination coefficients (k_b) were then determined from

$$k_b = \lambda_e - \lambda_p \, , \qquad (3)$$

where λ_p is the physical decay constant for the radionuclide in question.

The turnover time of an element previously has been defined as the reciprocal of the biological elimination coefficient (Reichle 1967). This value ($1/k$) represents the time required for the complete turnover of 100% of a nutrient pool in a given compartment. Each arthropod species in this study represented a separate compartment, and each had a characteristic turnover rate for different elements. When approximately 100% of an element in the food was assimilated, the value k_b represented the turnover rate for that element in that particular tissue. However, when appreciable amounts of the element were not assimilated, an approximate turnover rate (k') was determined from

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$$k' = \frac{k_1 \cdot k_2}{p_1 k_2 + p_2 k_1}, \qquad (4)$$

where $p = a$ of equation 1 when $t \to 0$ (single feeding). In the present study, all turnover rates for the two-component model (equation 1) were determined by the above method. When application of the single-component model was required, k_b was used as the turnover rate.

An estimate of the error associated with each k_b was obtained by applying the variance of the regression coefficient (λ_e) to k_b:

$$k_b \pm \hat{\sigma}_{k_b}{}^2 = (\lambda_e \pm \hat{\sigma}_{\lambda_e}{}^2) - \lambda_p \ . \qquad (5)$$

Nutrient analyses

Subsamples of previously dried arthropod and vegetative material collected during biomass determinations were ground with a mortar and pestle, redried at 105°C for 2 hr, weighed to the nearest 0.01 mg, ashed in a muffle furnace at 450°C for 32 hr, and finally dissolved in 0.1 N HCl for analysis in a Coleman Model 21 flame photometer with a propane-oxygen flame. A detailed description of the methodology employed in this analysis was given by Reichle, Shanks, and Crossley (1969).

Respirometry

Respiratory rates of *M. sanguinipes, C. fasciatus, P. fasciatus,* and *Lycosa rabida* Walckenaer were determined in a Gilson differential and a Phillipson continuous-reading respirometer. The respiratory rates were measured at 15°, 20°, and 25°C in 25- and 100-ml respiration chambers containing 1 ml of 5% KOH as a CO_2 absorbent. Adults were collected from the field site and acclimated to the experimental temperatures for 72 hr before respiration was determined. Respiration was determined for one individual per respirometer. The data were recorded as μliters O_2 consumed per hour and as μliters O_2 consumed per hour per milligram dry body weight.

Before extrapolation of respiratory rates to field populations, corrections were made for the mean daily field temperature prevailing during the sampling periods. These field temperatures were obtained from a weather station situated in the field area and operated by the U. S. Weather Bureau.

Caloric equivalents

A microbomb calorimeter (Phillipson 1964) was used for the caloric determinations of arthropod and plant samples that were collected through the year. All field samples were prepared for bomb calorimetry by grinding the previously dried material in a small Wiley mill and then subjecting them to an additional 2 hr of drying (105°C). The samples were then cooled and stored in dessicators containing $CaCl_2$.

Weekly arthropod samples were pooled into monthly samples to provide enough material for analysis. Pooling was not necessary with plant materials. Three replicate samples for each time period were made on plant material, while two were made on the arthropod material. Pellet sizes prepared for calorimetry averaged 14 mg. Results were expressed as calories per milligram ash free dry weight (AFDW).

Feeding rates and energy budgets

Insects.—Data obtained from the present study on field food consumption and food "preferences" were combined with energy budgets previously described for *Orchelimum fidicinum* Rehn and Hebard (Smalley 1960) and for *Melanoplus femur-rubrum* (De Geer) (Wiegert 1965) to construct energy budgets for *M. sanguinipes, C. fasciatus,* and *P. fasciatus.* A general budget for the Homoptera-Hemiptera was constructed based on feeding rates obtained from Wiegert (1964) for the spittlebug *Phileanus spumarius* L.

Food consumption in the field was determined for *M. sanguinipes, C. fasciatus,* and *P. fasciatus* in 1-m^2 enclosures containing ^{22}Na-tagged vegetation. The vegetation was tagged by inoculating the soil with 100 μCi of ^{22}Na per grass clump. The insects were introduced after sufficient activity had been translocated into the grass leaves. Animals were counted daily for determination of ^{22}Na activity. Feeding rates were determined from calculations based on the periodic concentrations of ^{22}Na in the insects and in the vegetation. The feeding habits were determined from observations of these three species in the field.

Feeding rates were determined gravimetrically in the laboratory (20°C) by feeding the insects fresh fescue shoots which had been placed in small vials of water. Food consumption was measured daily by correcting for evaporation and subtracting the remaining weight from the initial weight. *Pteronemobius* also feeds on litter; therefore, feeding rates were determined on litter as well as leaves for this species. Egestion rates were determined daily by collecting feces and drying them for 24 hr (105°C) before weighing. The insect dry weights were determined from the equations

Melanoplus
$Y = 0.059\ X^{1.272 \pm 0.057}$ $\quad N = 21 \quad r = 0.982$

Conocephalus
$Y = 0.427\ X^{0.927 \pm 0.091}$ $\quad N = 13 \quad r = 0.950$

Pteronemobius
$Y = 0.146\ X^{1.146 \pm 0.065}$ $\quad N = 14 \quad r = 0.981$

(where X = fresh weight, Y = dry weight, N = number of individuals, and r = correlation coefficient). Dry weights of leaves, litter, and feces were obtained from ovendrying. The dry weights obtained

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by means of these equations allowed data acquisition without sacrificing the animals. Caloric equivalents of animals, feces, and food were determined with the microbomb calorimeter. These results along with dry weights were used to construct the energy budgets.

Spiders.—An energy budget was also constructed for the wolf spider *Lycosa rabida*, which was fed nymphs of the brown cricket *Acheta domesticus* (L.). Adult lycosids were housed separately (20°C) in cages lined with aluminum foil and supplied with fresh water and cricket nymphs daily. Cricket remains were collected daily. Dry weights for spiders and crickets were determined from

Lycosa

$Y = 0.386\ X^{0.923 \pm 0.044}$ $N = 21$ $r = 0.978$

Acheta

$Y = 0.126\ X^{1.144 \pm 0.056}$ $N = 10$ $r = 0.991$

After 10 days spider feces were removed from the cages and dried for 24 hr (105°C). The caloric content of the cricket and spider carcasses and the spider feces was determined in the same manner as in the insect studies. The feeding habits of the spiders were based on field observations and also on data after Moulder (1969).

Statistical procedures

Seasonal differences in standing crop biomass and energy content for the four grassland vegetation components and for the four arthropod species were analyzed in a two-way factorial analysis of variance. Data on nutrient concentrations in vegetation and arthropods were analyzed with a three-way analysis. Prior to regression analyses, data from radioisotope-elimination studies, arthropod-metabolism studies, and feeding experiments were tested for homogeneity of variance (Draper and Smith 1966). Based on the results of these tests, either a linear or a nonlinear regression model was used. Tests of significance performed on the slopes obtained from the regression analyses were accomplished with formulae given in Steel and Torrie (1960). All summary statistics (e.g., mean, variance, and standard error) were determined with standard formulae (see Steel and Torrie 1960).

RESULTS AND DISCUSSION

Plant biomass

The maximum standing crop of grass biomass occurred in October (633 g/m²), of which 36% was living grass (*Festuca* and *Andropogon*) (Fig. 1). Dead biomass (standing dead plus litter) was greater than living biomass throughout the year. This phenomenon seems to be characteristic of early successional stages in old-field development where accumulation of dead material occurs more rapidly than decomposition, perhaps because of the small number of cryptozoan species found under these conditions.

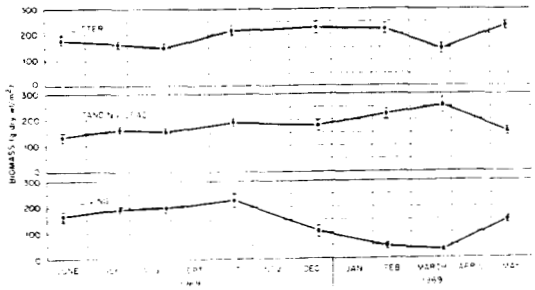

FIG. 1. Total standing crop biomass of living and dead grass in an eastern Tennessee *Festuca* meadow. The points shown represent means of 12 determinations with one standard error of the mean.

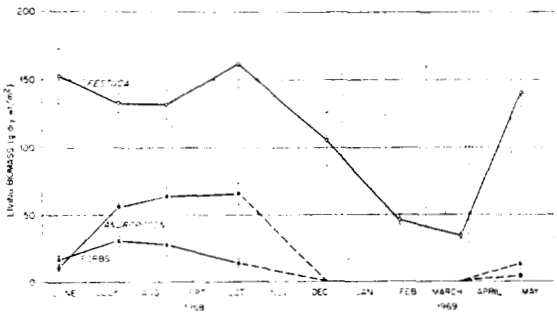

FIG. 2. Total living biomass (g dry wt/m²) of vegetation in an eastern Tennessee *Festuca* meadow. The points are means of 12 determinations with one standard error of a mean.

The dead biomass, therefore, exceeds the living throughout the annual cycle. The standing dead biomass ranged from 133 g/m² in June to a maximum of 256 g/m² in March (Fig. 1). The biomass of litter was minimal in August (149 g/m²) and reached a maximum (237 g/m²) in May.

The aboveground living biomass of the dominant plant species (*Festuca*) was high (153 g/m²) in early summer during the fruiting period and then declined, probably because of rapid loss of the fruiting stalks (Fig. 2). Top biomass then increased during the summer and fall and reached a maximum in October (170 g/m²). This peak was followed by an abrupt decline in biomass through the winter to a low of 34 g/m² in March. This type of growth cycle has been reported for *Festuca* by Hughes, Heath, and Metcalf (1951).

The standing crop of *Andropogon* was 8 g/m² in June 1968 (Fig. 2). The living portion of the broomsedge then increased in biomass through the summer and early fall and finally reached a maximum in October (65 g/m²) at the time of flowering. Occurrence of the maximum standing crop at flowering time has been discussed in some detail by Golley (1965) and Harris (1966). The living biomass then decreased to about 1 g/m² in December; new growth was not initiated until early April of the following year.

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TABLE 1. Density (number/m²) and biomass (mg dry wt/m²) of arthropod species in the grassland ecosystem during the 1968–69 growing season (values are weekly means of eight random 0.25-m² samples corrected to 1 m²)

Year and month	Week	Gryllidae *Pteronemobius*		Acrididae *Melanoplus*		Tettigonidae *Conocephalus*		Lycosidae *Lycosa*		Lycosidae *Schizocosa*		Oxyopidae *Oxyopes*		Hemiptera Homoptera	
		Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
1968..... J	28	14.0	29.40	8.0	78.21	3.5	10.17	3.5	82.75	1.5	4.98	1.0	3.84	8.0	18.52
	29	15.5	22.89	7.0	34.66	5.0	54.79	9.5	159.01	0.0	0.00	0.0	0.00	18.5	23.32
	30	25.0	78.16	7.0	44.57	2.0	11.66	3.5	62.63	0.0	0.00	0.5	1.36	18.5	25.86
	31	—[a]	—	—	—	—	—	—	—	—	—	—	—	—	—
1968..... A	32	15.0	83.93	8.5	141.23	2.5	76.24	1.5	31.39	0.0	0.00	1.0	2.75	0.5	0.84
	33	11.0	80.00	4.5	101.19	4.0	124.14	1.5	25.92	0.0	0.00	1.0	4.62	1.5	5.29
	34	11.5	143.98	8.0	283.24	6.0	340.14	0.5	10.25	0.0	0.00	0.0	0.00	2.5	5.70
	35	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1968..... S	36	7.5	168.19	5.0	394.72	3.0	162.77	0.5	5.69	0.0	0.0	0.0	0.00	0.0	0.00
	37	8.0	129.79	6.0	554.35	4.0	213.23	1.5	52.75	0.0	0.00	0.0	0.00	0.0	0.00
	38	8.5	178.73	4.0	504.87	3.0	214.82	4.5	218.21	0.0	0.00	0.0	0.00	0.0	0.00
	39	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1968..... O	40	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	41	8.0	176.24	6.5	859.81	2.0	114.27	0.5	8.34	0.0	0.00	0.0	0.00	1.5	17.82
	42	3.0	35.87	6.5	977.71	2.0	119.11	2.5	206.79	0.0	0.00	0.0	0.00	0.0	0.00
	43	3.0	51.78	6.5	784.79	0.0	0.00	2.0	218.88	0.0	0.00	0.0	0.00	0.5	5.81
	44	1.0	24.60	1.0	179.92	1.0	55.48	0.5	27.97	0.0	0.00	0.0	0.00	0.0	0.00
1968..... N	45	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	46	2.5	2.25	0.5	52.25	0.0	0.00	1.0	2.38	0.0	0.00	0.0	0.00	0.0	0.00
	47	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	48	0.0	0.00	0.0	0.00	0.0	0.00	1.5	22.31	0.0	0.00	0.0	0.00	0.0	0.00
1968..... D	49	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	50	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
	51	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	52	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1969..... J	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	3	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1969..... F	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	8	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
	9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1969..... M	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	12	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	13	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	1.0	1.21	1.5	0.29	0.0	0.00
1969..... A	14	0.0	0.00	0.0	0.00	0.0	0.00	2.0	15.13	0.5	0.72	0.0	0.00	0.0	0.00
	15	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	1.0	2.10	0.0	0.00	0.0	0.00
	16	0.0	0.00	0.0	0.00	0.0	0.00	4.5	21.82	1.5	4.30	0.0	0.00	0.5	1.10
	17	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	18	0.0	0.00	0.0	0.00	0.0	0.00	4.0	26.83	1.0	2.48	0.0	0.00	0.0	0.00
1969..... M	19	2.5	2.48	0.0	0.00	0.5	1.00	2.0	5.61	0.0	0.00	0.0	0.00	1.0	34.28
	20	0.0	0.00	0.0	0.00	0.0	0.00	4.5	19.45	1.5	4.59	1.0	1.06	1.5	0.63
	21	4.0	7.16	0.0	0.00	0.5	0.95	1.0	3.61	1.0	4.33	4.5	5.44	1.5	2.93
	22	2.0	3.38	0.0	0.00	1.5	1.29	2.0	4.10	1.0	2.83	5.0	6.52	12.5	1.56
1969..... J	23	2.5	6.75	0.0	0.00	11.5	6.73	0.0	0.00	0.5	5.17	4.5	9.01	12.5	6.28
	24	4.0	9.99	1.5	1.16	31.5	26.19	0.5	5.39	0.0	0.00	4.5	10.96	12.5	18.67
	25	4.0	9.52	2.5	3.16	50.0	65.86	2.5	27.85	0.0	0.00	2.5	6.18	4.3	17.93
	26	4.5	10.34	4.5	9.23	84.5	128.09	1.0	11.16	0.0	0.00	5.5	17.44	12.0	16.65
1969..... J	27	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[a]No sample taken.

The green forb standing crop reached a maximum in July (32 g/m²), then declined throughout the remainder of the growing season, and disappeared by mid-December (Fig. 2). When the standing crop of green forbs was greatest, it represented only 14% of the total living biomass. The species composition and flowering dates for these forbs were given by Van Hook (1970). Differences ($P \leq 0.05$) in the standing crop biomass were significant between the four major vegetational components as well as seasonal differences for each of the components.

Arthropod density and biomass

The population density and biomass of the major grassland species are given in Table 1. Percentage of total arthropod biomass was used as an index to

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evaluate the more important species in the community. The Homoptera and Hemiptera were grouped together because the biomass of each group was representative of only a small portion of the total and individually was not sufficient to permit separate analyses. Common homopteran families collected were Cicadellidae, Membracidae, Cercopidae, and Aphididae; the Miridae, Reduviidae, Coreidae, and Pentatomidae were the common hemipterans collected. Other insect species occurred in the weekly samples, but their biomass was too low for consideration as a major component of the food web. A checklist of the species collected from the grassland ecosystem was given by Van Hook (1970).

Biomass data for the grassland complex shows that orthopterans were the most important invertebrate herbivore species, whereas the major invertebrate predators were spiders belonging to the genus *Lycosa*. *Schizocosa* and *Oxyopes* (also spiders) were present primarily in the spring and early summer.

Lycosa biomass in the study area was highest during the summer and early fall months (July through October) and finally decreased in November (Fig. 3). The increase in *Lycosa* biomass in June lagged slightly behind the increase in biomass of the Homoptera-Hemiptera populations (May), which later declined in August. However, the biomass of the *Melanoplus, Conocephalus,* and *Pteronemobius* populations increased in July, August, and September and constituted an adequate source of nutrients and energy available for utilization by *Lycosa* predators. In September the biomass of *Conocephalus* and *Pteronemobius* populations began to decline while the *Melanoplus* biomass continued to increase to its maximum value in October (Fig. 3). Apparently the large biomass of the *Melanoplus* population and those prey species not included in this study (i.e., insect larvae) were adequate to sustain the *Lycosa* population even though the remaining prey populations were declining. All predator and prey populations declined in November.

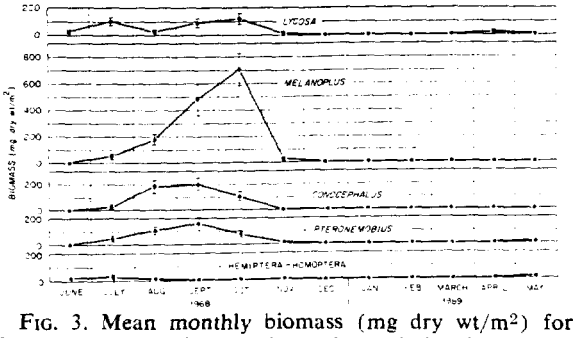

FIG. 3. Mean monthly biomass (mg dry wt/m²) for five components of the arthropod population in a grassland ecosystem. Points are means of 32 random samples taken during the month with one standard error of the mean.

Although individuals of the genus *Lycosa* live for several years (Kaston 1948), none were collected during the winter sampling periods presumably because *Lycosa* burrow into the soil or under grass clumps during periods of extreme temperature. This phenomenon explains in part the low biomass recorded for *Lycosa* in August when litter temperatures approached 50°C.

Population densities of grassland spiders have been examined by Baweja (1939), who reported 39 individuals/m² on grass plots. Bristowe (1939) found 559 spiders/m² in a meadow, and Duffey (1962) estimated 840/m² in a *Festuca*-dominated grassland. An estimate of 56/m² in the present study falls within this broad range. Biomass data on grassland spiders are almost completely lacking. Turnbull (1966) reported a spider biomass of 220 mg/m² for an overgrazed pasture in Canada and estimated spiders to comprise 30% of the total arthropod biomass. Menhinick (1967) reported that spiders constituted 13% of the total arthropod biomass in a lespedeza community. In the present study spiders had a maximum biomass of 146 mg/m², which accounted for 15% of the total arthropod biomass in the *Festuca-Andropogon* community.

In a study of grasshopper populations Wiegert (1965) found a maximum density of 2.5 individuals/m² and a maximum biomass of 60 mg/m² for *Melanoplus* in a Michigan old field. Odum, Connell, and Davenport (1962) found a maximum standing crop of 350 mg/m² for *Melanoplus* on an old field in Georgia. Smalley (1960) reported 175 mg/m² for *Orchelimum* in a Georgia salt marsh. In the present study the maximum *Melanoplus* biomass was estimated to be 705 mg/m²; *Conocephalus*, a tettigoniid, had a maximum biomass of 200 mg/m² in the same grassland community (Fig. 3). Data on field cricket density and biomass are lacking in the literature; a maximum value of 175 mg/m² was found for *Pteronemobius* in this investigation.

Homoptera-Hemiptera populations have been studied less extensively than the Orthoptera. Wiegert (1964) reported a maximum biomass of 24 mg/m² for the meadow spittlebug *Philaenus spurmarius* L. in a Michigan old field. Menhinick (1967) found the combined Homoptera-Hemiptera biomass in a lespedeza stand to be 22 mg/m². A maximum combined value of 22 mg/m² for the Homoptera-Hemiptera populations was found in the present study (Fig. 3).

Radioisotope retention

The measurement of radioisotope assimilation by arthropods provides a technique whereby estimates of the digestive assimilation of nutrients not obtainable from conventional nutrient budgets can be determined (Reichle 1969). Biological turnover rates were used to estimate nutrient concentrations in

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TABLE 2. Biological elimination coefficients (k_{b_1} and k_{b_2}) of unassimilated (p_1) and assimilated (p_2) ^{47}Ca, ^{42}K, and ^{22}Na in four species of grassland arthropods (values are means with one standard error in parentheses)

Species[a]	^{47}Ca				^{42}K[b]		^{22}Na[b]	
	k_{b_1} days^{-1}	p_1 %	k_{b_2} days^{-1}	p_2 %	k_{b_2} days^{-1}	p_2 %	k_{b_2} days^{-1}	p_2 %
Pteronemobius	(N = 10)							
15°C	1.232 (0.318)	39.9	0.124 (0.038)	60.1	0.247 (0.026)	100.0	0.042 (0.004)	100.0
20°C	4.776 (0.218)	31.6	0.149 (0.005)	68.4	0.339 (0.023)	100.0	0.078 (0.005)	100.0
25°C	6.865 (4.421)	14.7	0.274 (0.028)	85.3	0.517 (0.025)	99.8	0.092 (0.008)	100.0
Melanoplus	(N = 6)							
15°C	1.759 (0.287)	71.8	0.362 (0.151)	28.2	0.256 (0.020)	100.0	0.012 (0.002)	99.2
20°C	2.337 (0.282)	82.6	0.493 (0.263)	17.4	0.267 (0.019)	100.0	0.067 (0.012)	97.9
25°C	4.260 (0.712)	31.7	0.549 (0.036)	68.3	0.697 (0.038)	100.0	0.034 (0.004)	100.0
Conocephalus	(N = 6)							
15°C	1.093 (0.168)	78.1	0.202 (0.022)	21.9	0.071 (0.022)	100.0	0.053 (0.006)	100.0
20°C	1.363 (0.367)	42.2	0.235 (0.013)	58.8	0.125 (0.013)	100.0	0.085 (0.011)	98.9
25°C	5.607 (0.987)	36.9	0.353 (0.024)	63.1	0.173 (0.017)	100.0	0.139 (0.011)	100.0
Lycosa	(N = 5)							
15°C	—[b]	—[b]	0.007 (0.003)	100.0	0.081 (0.016)	100.0	0.039 (0.006)	96.2
20°C	—[b]	—[b]	0.008 (0.003)	100.0	0.118 (0.007)	99.0	0.052 (0.007)	97.2
25°C	—[b]	—[b]	0.014 (0.003)	100.0	0.170 (0.027)	98.0	0.069 (0.005)	96.7

[a]The radioactive tracer material was administered to each species through the food chain: *Pteronemobius* was fed tagged grass litter, *Melanoplus* and *Conocephalus* tagged grass leaves, and *Lycosa* tagged crickets.
[b]No first component.

feces. Biological elimination coefficients (k_b = turnover rate) and per cent assimilation (p_2) were calculated for ^{47}Ca, ^{42}K, and ^{22}Na in four grassland arthropod species (Table 2). Calcium-47 retention followed the two-component model (equation 1) and the assimilated fraction (p_2) ranged from 17.4% for *Melanoplus* to 100% for *Lycosa*. The increase in assimilation (p_2) with temperature for the three species of Orthoptera tagged with ^{47}Ca is not consistent with the results of Hubbell, Sikora, and Paris (1965) and O'Neill (1967). They found that assimilation/ingestion energy ratios for isopods and millipedes decreased with increased temperature and attributed this to a more rapid passage of food through the intestional tract with increased metabolic activity. They further found that at lower temperatures and prolonged food retention, the assimilation of energy increased. Nutrient assimilation and energy assimilation are accomplished by different physiological mechanisms which perhaps differ in respect to temperature dependence. Assimilation of ^{42}K and ^{22}Na was nearly complete in all species at each experimental temperature (Table 2), indicating that retention followed the one-component model (equation 2). Values of k_b reported in Table 2 are within the ranges reported for arthropods in the review of radioisotope turnover in animals by Reichle, Dunaway, and Nelson (1970).

Since temperature has been reported to be the most important abiotic factor affecting biological turnover (Reichle and Crossley 1965), the values of k_b for each radioisotope in each arthropod species were regressed against temperature in the equation

$$Y = ae^{bX}, \qquad (6)$$

where $Y = k_b$, a = constant, b = slope, X = temper-

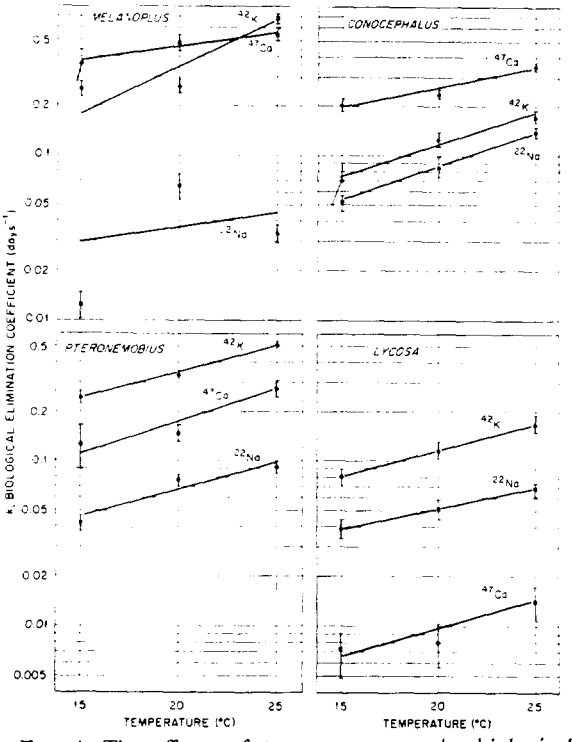

FIG. 4. The effects of temperature on the biological elimination of ^{47}Ca, ^{42}K, and ^{22}Na in four arthropod species. Each point represents the mean elimination coefficient with one standard error of the mean.

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ature (°C), and e = the base of the natural logarithm. The results of these analyses are presented in Fig. 4. The slopes (b) of each of the curves were tested against the slope of a $Q_{10} = 2$ relationship. Based on these data no differences were detected ($P \leq 0.05$), indicating that a 10°C rise in temperature would cause a twofold increase in excretion rate. Similar results have been shown for different radioisotopes in other arthropod species (Reichle 1967, Reichle and Crossley 1967, Moulder 1969).

The k_b value for a radioisotope in a particular species under field conditions was calculated from equation 6 where each constant is associated with that particular radioisotope-species combination, b = 0.0693 (slope of $Q_{10} = 2$) and X = the selected field temperature (°C). These calculations were actually valid only within the temperature limits used in the laboratory. The turnover rates were used to evaluate the movement of stable calcium, potassium, and sodium through each of the arthropod species studied. This procedure was helpful in arriving at a clearer understanding of the transient behavior of these elements in secondary and tertiary trophic levels.

Nutrient concentrations

Vegetation.—Concentrations of sodium, calcium, and potassium were determined in the living, standing dead, and litter components of the *Festuca-Andropogon* complex and in forbs in the study area (Table 3). Ash composition (Table 4) differed among the components of vegetation and through time for each component ($P \leq 0.05$). Expressing results on an ash-free dry weight basis (AFDW) removes differences among components due to ash-composition differences and permits direct comparisons of nutrient content of each element independent of other elements (Reichle et al. 1969).

Analysis of variance demonstrated significant differences ($P \leq 0.05$) among components and through time for sodium, calcium, and potassium concentrations in the grassland vegetation. Characteristically, potassium is the nutrient found in highest concentrations in green vegetation. In *Festuca-Andropogon* and green forbs, the mean concentration was 14.28 mg/g AFDW. This nutrient, generally stored as salts in vacuolar sap, is lost at fairly rapid rates by leaching, and relatively low concentrations (2.46 mg/g

TABLE 3. Concentrations of sodium, calcium, and potassium in the living, standing dead, litter, and forb components of the vegetation in an eastern Tennessee grassland ecosystem (values are means of four replicate determinations with one standard error of the mean in parentheses)

Date	*Festuca-Andropogon*			Forb
	Living	Standing dead	Litter	
		Sodium (mg/g ash free dry wt)		
June 1968	0.74 (0.12)	0.06 (<.001)	0.24 (<.001)	0.36 (0.02)
July "	0.86 (<.001)	0.61 (0.12)	0.22 (0.02)	0.31 (0.05)
Aug. "	0.79 (0.02)	0.59 (0.02)	0.30 (0.03)	0.21 (<.001)
Oct. "	1.37 (0.13)	0.39 (0.02)	0.13 (<.001)	0.20 (0.01)
Nov. "	1.07 (0.04)	0.16 (0.03)	0.17 (0.08)	0.53 [a]
Dec. "	0.71 (0.13)	0.14 (0.01)	0.10 (0.02)	0.22 (0.02)
Feb. 1969	0.05 (<.001)	0.06 (<.001)	0.06 (<.001)	0.09 (<.001)
March "	0.07 (<.001)	0.05 (<.001)	0.07 (<.001)	0.05 (<.001)
May "	0.09 (0.02)	0.07 (<.001)	0.04 (<.001)	0.08 (<.001)
		Calcium (mg/g ash free dry wt)		
June 1968	2.58 (0.20)	4.62 (0.06)	4.74 (0.12)	8.17 (0.67)
July "	2.69 (0.02)	4.10 (0.35)	4.53 (0.42)	10.51 (0.06)
Aug. "	2.98 (0.06)	4.09 (0.34)	5.62 (0.69)	10.53 (0.04)
Oct. "	2.35 (0.33)	4.31 (0.09)	5.75 (0.15)	14.49 (0.09)
Nov. "	3.12 (0.04)	4.78 (1.47)	5.44 (0.13)	9.59 [a]
Dec. "	2.27 (0.07)	3.62 (0.09)	5.09 (0.35)	11.13 (1.54)
Feb. 1969	1.50 (0.02)	5.04 (0.11)	6.27 (0.04)	6.69 (0.11)
March "	1.77 (0.01)	3.59 (0.05)	4.77 (0.10)	4.67 (0.33)
May "	2.24 (0.16)	5.52 (0.12)	3.87 (0.36)	7.44 (0.05)
		Potassium (mg/g ash free dry wt)		
June 1968	15.11 (0.22)	3.78 (0.16)	2.61 (0.06)	19.77 (0.47)
July "	15.79 (0.05)	3.68 (0.52)	2.58 (0.19)	13.31 (0.24)
Aug. "	21.95 (0.81)	5.79 (0.43)	4.33 (0.19)	13.74 (0.13)
Oct. "	16.48 (0.31)	2.54 (0.33)	1.62 (0.02)	11.14 (0.14)
Nov. "	20.18 (0.11)	1.06 (0.14)	0.93 (0.05)	10.91 [a]
Dec. "	18.78 (0.10)	1.73 (0.02)	1.14 (0.04)	3.38 (0.03)
Feb. 1969	15.39 (1.05)	2.07 (0.04)	1.25 (0.04)	2.27 (<.001)
March "	18.19 (0.56)	3.45 (0.11)	1.40 (0.03)	1.55 (0.15)
May "	21.88 (2.56)	3.02 (0.06)	1.30 (<.001)	17.39 (0.31)

[a] One sample

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TABLE 4. Ash composition (percentage of dry weight)[a] of four vegetation components and four arthropod species inhabiting the grassland ecosystem

Date	Vegetation			Forbs
	Festuca-Andropogon			
	Living	Standing dead	Litter	
June 1968	7.60	10.81	8.41	9.40
July "	8.44	7.03	8.99	9.14
Aug. "	10.76	7.95	17.21	8.51
Oct. "	8.60	7.80	16.04	13.57
Nov. "	8.72	7.81	12.11	8.74
Dec. "	8.31	7.34	10.91	7.08
Feb. 1969	7.34	12.69	19.36	6.37
March "	7.59	7.52	15.26	3.48
April "	9.29	9.94	10.62	7.86

Arthropods

Date	*Pteronemobius*	*Melanoplus*	*Conocephalus*	*Lycosa*
June 1968	3.23	1.91	1.44	5.51
July "	3.59	1.82	2.69	2.41
Aug. "	1.98	1.86	1.65	2.20
Sept. "	1.67	1.32	1.47	2.01
Oct. "	2.09	1.43	1.79	2.15
Nov. "	2.95	1.37	[b]	4.50
April 1969	[b]	[b]	[b]	1.77
May "	1.98	[b]	3.24	2.71

[a]Ash weights are based on exposure to 450°C for 32 hr.
[b]None present in sample.

AFDW) are therefore found in dead material (standing dead + litter). Calcium is usually found in greatest concentrations in the leaves of plants, especially older leaves. The most abundant forms are fixed pectate salts in the middle lamella and insoluble calcium oxalate in the vacuole. Mean calcium concentration in green components of grassland vegetation was 5.83 mg/g AFDW. Because of the very low leaching rates of fixed and insoluble calcium, the level of this element remained relatively high in dead vegetation (4.77 mg/g AFDW). Sodium, for which there appears to be no essential metabolic need in plants, remained low in both green (0.43 mg/g AFDW) and dead (0.19 mg/g AFDW) vegetation. These results are consistent with the data summarized by Miller (1958). For mixed grasses and forbs he reported mean values of 14.2 mg/g dry wt for potassium, 5.0 mg/g dry wt for calcium, and 1.85 mg/g dry wt for sodium. Sodium and potassium levels in timothy grass of 0.9 and 28.4 mg/g dry wt, respectively, were reported by ap Griffith and Walters (1966).

Arthropods.—Nutrient concentrations were determined in the four major grassland arthropod species (Table 5). Since the values are means of two replicate determinations on the same sample, any estimate of error would reflect efficiency of analyses and not biological variability. Hence, the standard errors are not included. Ash composition (Table 4) differed among species ($P \leq 0.05$), but not through time for each species. Reduction to a common scale (AFDW) again allowed direct comparisons between species.

Whole-body concentrations of sodium, calcium, and potassium of the families Miridae and Cicadellidae were determined from analyses of pooled spring samples. Material was not sufficient for temporal analyses for these families. Sodium content of Miridae (1.28% ash) was 2.02 mg/g AFDW; calcium, 1.34 mg/g AFDW; and potassium, 2.01 mg/g AFDW. For Cicadellidae (1.26% ash) sodium concentration was 1.22 mg/g AFDW; calcium, 0.71 mg/g AFDW; and potassium, 4.78 mg/g AFDW.

Analysis of variance demonstrated no significant differences among species or through time for sodium, calcium, and potassium for the species reported in Table 5. Concentrations of sodium and calcium in the Miridae and Cicadellidae did not differ from those in the three herbivore species. However, potassium concentrations in the families Miridae and Cicadellidae were higher ($P \leq 0.05$) than those of the other herbivores. These higher levels of potassium could result from the method of feeding used by the Homoptera and Hemiptera. Potassium is known to occur in plants principally as soluble inorganic and organic salts in the plant cells (Meyer, Anderson, and Bohning 1960). The sucking insects

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TABLE 5. Monthly variation in concentrations of sodium, calcium, and potassium in the four major arthropod species collected from the grassland ecosystem (values are means of two determinations on the same pooled sample)

Date	*Pteronemobius*	*Melanoplus*	*Conocephalus*	*Lycosa*
	Sodium (mg/g ash free dry wt)			
June 1968	1.48	1.70	0.92	3.33
July "	0.56	0.87	1.26	0.29
Aug. "	0.90	0.28	0.21	0.62
Sept. "	0.42	0.25	0.28	0.29
Oct. "	0.74	0.27	0.36	0.27
Nov. "	1.15	1.17	—	4.39
April 1969	—[a]	—	—	2.53
May "	2.75	—	1.69	3.83
	Calcium (mg/g ash free dry wt)			
June 1968	1.55	2.29	0.27	1.25
July "	0.72	0.98	0.47	0.69
Aug. "	0.56	0.54	0.19	0.68
Sept. "	0.83	0.32	0.24	0.48
Oct. "	1.16	0.43	0.24	0.56
Nov. "	1.17	0.21	—	0.99
April 1969	—	—	—	1.16
May "	1.23	—	1.02	1.22
	Potassium (mg/g ash free dry wt)			
June 1968	2.01	1.23	0.12	1.69
July "	0.44	1.45	0.29	0.31
Aug. "	0.84	0.53	0.19	0.44
Sept. "	0.49	0.49	0.31	0.38
Oct. "	1.66	0.54	0.32	0.67
Nov. "	0.76	0.73	—	3.63
April 1969	—	—	—	3.83
May "	3.20	—	1.16	4.71

[a]None present in sample.

pierce the epidermal cell layers and ingest intracellular juices (high in potassium). Chewing insects dilute their potassium intake with macerated plant parts thus reducing total body burden of this element.

Discussion of energy or nutrient concentrations is more meaningful in an ecological context if the trophic level concept is utilized. In this and following discussions, however, the term predator trophic level applies only to the family Lycosidae. Likewise, the term herbivore trophic level applies only to the orders Orthoptera, Hemiptera, and Homoptera. Other members of each trophic level were present in the system, but they were not present in sufficient biomass to warrant consideration (see Table 1).

The mean annual concentration of sodium in the predator trophic level (1.94 mg/g AFDW) was higher ($P \leq 0.05$) than the concentration in the primary consumer level (1.18 mg/g AFDW). This represents a concentration factor of 1.64 between trophic levels which is in good agreement with the value of 1.51 reported for a saprovore-predator trophic transfer (Reichle et al. 1969). Herbivore sodium content was much higher ($P \leq 0.01$) than the sodium concentration of the primary producers (0.43 mg/g AFDW). The omnivore included in this study, *Pteronemobius*, was very much higher ($P \leq 0.001$) in sodium concentration than its detritus food base (0.19 mg/g AFDW). Mean annual whole-body content of calcium did not increase significantly ($P \leq 0.05$) from the herbivore (0.85 mg/g AFDW) to predator (0.88 mg/g AFDW) trophic levels. Calcium content was much less in these levels than in the primary producers (5.82 mg/g AFDW). Mean calcium concentration for all arthropods studied was 33.5 mg/g ash wt. This value agrees well with the data summarized by Clark (1958). No difference ($P \leq 0.05$) was determined between herbivore (1.87 mg/g AFDW) and predator (1.96 mg/g AFDW) trophic levels for potassium. Both, however, were very much lower ($P \leq 0.001$) than the primary producer level (14.28 mg/g AFDW). These data are somewhat inconsistent with the results reported by Reichle and Crossley (1969) for a detritus-saprovore-predator trophic transfer. Saprovores included in their study included millipedes (*Apheloria, Cambala, Dixidesmus, Ptyloiulus,* and *Scytonotus*); crickets (*Ceuthophilus* and *Nemobius*); beetle (*Geotrupes*); wood roach (*Parcoblatta*); isopod (*Ligidium*); and the phalangid *Leiobunum*. Predator species included spiders (Lycosidae and Ctenizidae); beetles (*Dicaelus, Evarthrus, Hololepta, Sphaeroderus,* and *Staphylinus*); and the centipede *Otocryptops*. The potassium content of saprovores was 3.51 times higher than the level in detritus and 1.8 times that of the predators. The saprovores concentrated potassium in that system. In the grassland, potassium levels are apparently high enough in the vegetation to require no further concentration by the herbivores.

Nutrient flux (NI_{ij} = mg nutrient/m^2 per day) from some food source i to a consumer j was determined by substituting Q_i = the concentration of nutrient in the food source i (mg/mg dry wt) for CE_i in equation 12. The rate of nutrient loss (NE_{jk} = mg nutrient m^2 per day) from a consumer via fecal material was estimated by

$$NE_{jk} = (k_h \cdot Q_j + a_1 \cdot Q_i \cdot I_j)\, x_j\,, \qquad (7)$$

where k_h = the biological elimination coefficient for the element and animal species in question, Q_j = the concentration of the nutrient in the consumer, a_1 = the fraction of the element that is unassimilated, I_j = the ingestion rate for the consumer (mg food/mg dry wt animal per day), and x_j = the consumer biomass (mg/m^2). In cases where there was complete assimilation of an element ($a_1 = 0$), the second term of equation 7 ($a_1 \cdot Q_i \cdot I_j$) was omitted.

Arthropod metabolism

At 20°C *Pteronemobius* had the highest oxygen consumption rate (μliter O_2/mg per hour) and was followed in decreasing order by *Melanoplus, Cono-*

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TABLE 6. Oxygen consumption (maintenance metabolism) of four of the dominant arthropod species from an eastern Tennessee grassland ecosystem (values in parentheses are one standard error of the mean)

Species	Temperature (°C)	Number of animals	Per cent moisture[a]	Mean μliter O_2/hr per animal	Mean μliter O_2/hr per milligram	Total O_2[b] / Maintenance O_2
Pteronemobius fasciatus	15	14		35.29 (2.71)	1.32 (0.08)	
	20	14	71.6	69.78 (6.92)	2.37 (0.11)	1.85
	25	14		83.23 (8.35)	3.18 (0.14)	
Melanoplus sanguinipes	20	27	73.1	165.47 (22.42)	1.58 (0.18)	2.94
Conocephalus fasciatus	20	10	72.1	89.89 (7.31)	1.75 (0.07)	2.08
Lycosa rabida	15	10		51.48 (5.19)	0.72 (0.06)	
	20	8	74.9	49.07 (6.47)	0.96 (0.06)	3.57
	25	9		77.20 (7.22)	1.49 (0.07)	

[a]Moisture content was determined at 105°C for 24 hr.
[b]Total oxygen consumption was estimated in the determination of energy budgets (Table 9 and accompanying text). This ratio of total to maintenance metabolism was used to correct the values given above for locomotor activity.

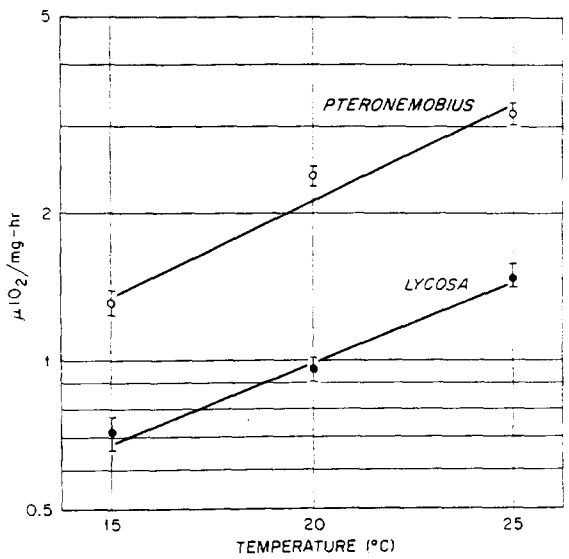

FIG. 5. The effect of temperature on the metabolism of *Pteronemobius fasciatus* and *Lycosa rabida*. Points are means with one standard error of a mean.

cephalus, and *Lycosa* (Table 6). The metabolic rate of *Lycosa* was 1.6 to 2.4 times less than the prey species. The respiratory rate approximately doubled in *Pteronemobius* and *Lycosa* when the temperature was increased from 15° to 25°C. The relationship between metabolic rate and temperature for *Pteronemobius* and *Lycosa* (Fig. 5) was determined from a regression analysis of equation 6 where Y = oxygen consumption rate (μliter/mg per hour), a = constant, b = slope, and X = temperature (°C). The values of a and b for *Pteronemobius* were 0.219 and 0.076 respectively, and for *Lycosa* a equaled 0.357 and b equaled 0.089. The slope values (b) were tested against the slope of a $Q_{10} = 2$ relationship, and based on these data both differences were nonsignificant ($P \leq 0.05$) indicating that the oxygen consumption rate doubled with a 10°C rise in temperature. On the basis of these results and those of Smalley (1960) and Wiegert (1965) for temperature dependence of metabolism for several grasshopper species, a slope of 0.0693 was used for temperature corrections of respiratory rates in subsequent calculations.

Arthropod metabolism has been described as roughly proportional to the two-thirds power of body size (Bornebusch 1930, Edwards 1946). This relationship is defined by

$$Y = aX^b \qquad (8)$$

where Y = metabolism (μliter O_2/hr), a = constant, b = slope = 0.67 relative to absolute weight, and X = body weight. Phillipson (1960) has shown that the metabolism of arthropods is affected by physiological and environmental factors so that a constant slope (0.67) does not hold true for all cases. The value of b should therefore be determined for each arthropod species.

The relationship between metabolism (Y) and body weight (X) of the four species of grassland arthropods studied is shown in Fig. 6. The curves are described as follows:

Melanoplus
$Y = 0.473\ X^{1.248 \pm 0.216}$ $N = 27$ $r = 0.756$

Conocephalus
$Y = 2.010\ X^{0.962 \pm 0.252}$ $N = 14$ $r = 0.803$

Pteronemobius
$Y = 2.636\ X^{0.965 \pm 0.159}$ $N = 14$ $r = 0.868$

Lycosa
$Y = 0.376\ X^{1.236 \pm 0.238}$ $N = 9$ $r = 0.904$

When all arthropod species studied were considered as one group,

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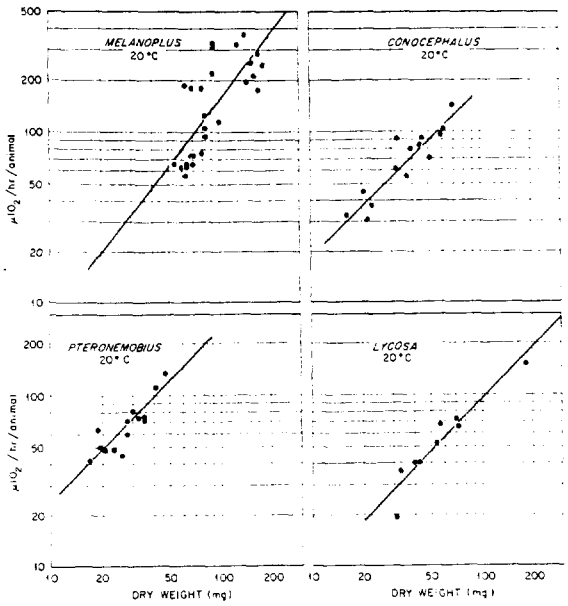

FIG. 6. The relationship between body weight and oxygen consumption for four arthropod species inhabiting the grassland ecosystem.

$$Y = 3.781\ X^{0.790 \pm 0.088} \qquad N = 64 \quad r = 0.766$$

defined the relationship. The value of b (slope) from this latter equation is in general agreement with the value of 0.84 reported for 15 forest-floor arthropod species (Reichle 1968) and nine grasshopper species (Wiegert 1965). The difference between the pooled value and the individual slope values was probably due to the limited size range used in the determinations for each species. Small animals were especially poorly represented in each group. Inclusion of small arthropods with relatively high metabolic rates would tend to lower the observed slope values for each of the species studied. The value of b for *Lycosa* (1.236) is similar to the value of 1.37 reported by Moulder (1969) for forest-floor spiders.

The value of expressing metabolism as a function of temperature and body weight is of especial interest, particularly in studies pertaining to the energetics and trophic dynamic relationships of ecological systems. Such a relationship was obtained in the present study by combining equations 6 and 8 and is shown as follows:

$$Y = aX^b e^{0.0693(T-20)}, \qquad (9)$$

where Y is μliter O_2/mg per hour, X is body weight, a = constant associated with equation 8, b = slope of equation 8, and T = °C. The value $(T - 20)$ was used rather than T because 20°C was the reference point (i.e., equation 8 was solved for the species studied at 20°C). Equation 9 was used to correct arthropod metabolism for temperature and body size when extrapolating to field conditions.

TABLE 7. Seasonal changes in the caloric content (cal/g ash free dry wt) of four vegetation components from a grassland ecosystem (values are means of six determinations with one standard error of the mean in parentheses)

Season	*Festuca-Andropogon* Living	*Festuca-Andropogon* Standing dead	*Festuca-Andropogon* Litter	Forbs
Spring	4,998 (177)	4,479 (170)	4,433 (116)	4,381 (48)
Summer	4,719 (94)	4,465 (188)	4,510 (124)	4,484 (80)
Fall	4,820 (56)	4,631 (91)	4,737 (127)	4,671 (150)
Winter	4,592 (148)	4,581 (141)	4,095 (85)	4,466 (93)

The total caloric value of the oxygen consumed during metabolic processes is essential in energy-flow studies. Caloric values were calculated by multiplying Y (μliter O_2/mg per hour) of equation 9 by the thermal equivalent of oxygen (0.0048 cal/μliter) assuming a respiratory quotient of 0.82 as suggested by Brody (1964) for bioenergetics studies.

Caloric relationships

Vegetation.—The energy content of the living grass portion of the sampled vegetation ranged from 4,592 to 4,998 cal/g AFDW (annual mean = 4,782 cal/g AFDW). The maximum value (4,998) occurred during the flowering period of *Festuca* (May and June). The caloric content then declined slightly before increasing to another high of 4,820 cal/g AFDW, which coincided with the flowering of *Andropogon* (August and September). The minimum energy values for *Festuca* occurred during the winter months. Golley (1965) reported a similar correlation between phenology and caloric content for a broomsedge community in South Carolina. The flowering time of forbs also has been reported to be the period of highest energy content (Kieckhefer 1962). The peak energy content of forbs was distributed evenly throughout the growing season about a mean of 4,500 cal/g AFDW. Variation in the energy content of forbs was not similar to that of grass, perhaps because several species were included in the analysis of the former.

Energy content of the standing dead component varied by almost 900 cal/g AFDW from a minimum in March (4,120 cal/g AFDW) to a maximum in August (5,016 cal/g AFDW). The relatively high value recorded in late summer was probably largely due to a pulse of fresh material produced during the flowering period of *Festuca*. The mean annual energy content of the litter component (4,646 cal/g AFDW) was somewhat higher than that of the standing dead. This phenomenon could be due to differential decomposition processes whereby certain low-energy litter components were initially removed, which resulted in a reduction in weight but an increase in caloric content on an AFDW basis.

The values reported in Table 7 agree closely with

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TABLE 8. Seasonal variation in caloric content (cal/g ash free dry wt) of four species of grassland arthropods collected during 1968–69 (values are means of four determinations with one standard error of the mean in parentheses)

Season	*Pteronemobius*	*Melanoplus*	*Conocephalus*	*Lycosa*
Spring	5,223 (227)	4,821 (133)	5,185 (134)	5,379 (176)
Summer	5,850 (93)	5,547 (116)	6,129 (120)	5,964 (265)
Fall	5,753 (125)	5,736 (358)	5,796 (236)	5,859 (210)

the caloric equivalents reported for grassland and old-field vegetation (Golley 1961, 1965, Wiegert and Evans 1964, Ovington and Lawrence 1967, Kucera, Dahlman, and Koelling 1967, Malone 1968).

Arthropods.—Energy content of the four species of arthropods from the grassland ecosystem was relatively low in early instars and then increased through development to a maximum just prior to egg laying (Table 8). Significant differences ($P \leq 0.05$) occurred both among species as well as through time for each species. Caloric equivalents for a number of arthropod species which constituted only a minor portion of the energy regime were: Miridae, 4,633 cal/g AFDW (1.28% ash); Cicadellidae, 5,351 cal/g AFDW (1.26% ash); Cercopidae, 5,768 cal/g AFDW (9.03% ash); Membracidae, 5,164 cal/g AFDW (2.20% ash); Aphididae, 5,123 cal/g AFDW (3.05% ash); and *Acheta domesticus* (L.), 5,727 cal/g dry wt. The caloric content of the feces of the dominant arthropod species were: *Melanoplus*, 3,945 cal/g dry wt; *Conocephalus*, 3,855 cal/g dry wt; *Pteronemobius*, 4,154 cal/g dry wt; and *Lycosa*, 3,667 cal/g dry wt.

The mean annual calorific equivalents determined from the data of Table 8 for the grasshoppers *Melanoplus* and *Conocephalus* combined and for the field cricket *Pteronemobius* were 5,536 and 5,634 cal/g AFDW, respectively. Caloric equivalents for *Melanoplus* of 5,151 and 5,203 cal/g dry wt have been reported by Cummins (1967) and by Wiegert (1965). Golley (1961) reported 5,363 cal/g dry wt as a mean value for *Schistocerca americana* (Drury), and Smalley (1960) estimated the mean caloric content of *Orchelimum* to be 5,536 cal/g dry wt. Moulder (1969) reported a value of 5,445 cal/g AFDW for *Schizocosa* (a lycosid), which is similar to the annual average of 5,693 cal/g AFDW for *Lycosa* in the present study. The mean Homoptera-Hemiptera caloric content determined in this study was 5,210 cal/g AFDW. A mean value of 5,829 cal/g dry wt was reported for the genus *Philaenus* (Homoptera) by Wiegert (1965).

Arthropod food relations and energy budgets

The laboratory and field experiments were combined to describe the feeding patterns of the herbivore and omnivore species *M. sanguinipes*, *C. fasciatus*, and *P. fasciatus*. Since each of these species fed with equal readiness on *Festuca* and *Andropogon*, these grasses were grouped into a single compartmental component. Forbs were preferred by the herbivores over *Festuca* and *Andropogon* by as much as a factor of two. *Pteronemobius* consumed moist litter equally as well as fresh grass shoots; however, dry litter was accepted only half as often as fescue shoots. Since no data were available for the Homoptera-Hemiptera component of the system, it was assumed that they fed equally well on grass or green forbs.

The feeding habits of wolf spiders (*Lycosa*) were determined by offering them a variety of prey species. Acceptance of the prey by spiders was based largely on the size of the prey, the "palatability" of the prey, prey abundance, and the activity of the prey species (Moulder 1969). Since each of these criteria varies seasonally, the food habits of *Lycosa* differed through the growing season. In the spring, populations of the prey species and the predator species were small, both in number and in individual size. During spring *Lycosa* had an equal "preference" for the nymphs of *Melanoplus*, *Conocephalus*, *Pteronemobius*, and several families comprising the Homoptera-Hemiptera grouping (Cicadellidae, Cercopidae, Miridae, and Pentatomidae). As the season progressed, these nymphs grew to adults and their habitats became more stratified. During summer *Melanoplus* and *Conocephalus* moved into the herb stratum and became more difficult for the spiders to capture, *Pteronemobius* was observed to be as "catchable" as during spring, and certain of the Homoptera-Hemiptera species (Miridae and Cercopidae) appeared to become easier to capture, probably because of an associated increase in size and speed of *Lycosa*. By fall *Melanoplus* had become almost too large (on an individual basis) for *Lycosa* to successfully capture, whereas *Conocephalus* and *Pteronemobius* appeared to remain as "catchable" as during the summer. Representative species of the Homoptera-Hemiptera were observed to be somewhat more "catchable" during fall than during summer.

Calculation of energy intake rates (equation 12) depends in part on the quantification of the data on *Lycosa* feeding preferences. Quantification of these types of data can be achieved in laboratory experiments (O'Neill 1969), but under field conditions quantitative assessment of predator feeding preferences is extremely difficult to achieve. In the present study a superficial quantification of *Lycosa* feeding preferences was based on results of the prey-acceptance studies in the laboratory and on observations of these predators in the field. Stated as a proportion of the total diet, the feeding preferences of *Lycosa* for *Melanoplus*, *Conocephalus*, *Pteronemobius*, and the Homoptera-Hemiptera were estimated

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TABLE 9. Energy budgets for the adult stage of three of the dominant grassland arthropod species (budgets based on data collected from 10 individuals of each species during late summer)

Species		Ingestion (I)	Egestion (E)	Assimilation (A)	Production (P)	Respiration (R)
Pteronemobius (grass)[d]	mg/mg per day[a]	0.40	0.24	0.16	0.01	
	cal/mg[b]	4.42	4.15	4.88	4.79	
	cal/mg per day[c]	1.77	0.99	0.78	0.05	0.73
Pteronemobius (litter)	mg/mg per day	0.40	0.24	0.16	0.01	
	cal/mg	3.86	4.15	3.44	4.79	
	cal/mg per day	1.54	0.99	0.55	0.05	0.50
Conocephalus (grass)	mg/mg per day	0.28	0.20	0.08	0.01	
	cal/mg	4.42	3.86	5.88	4.78	
	cal/mg per day	1.24	0.77	0.47	0.05	0.42
Lycosa (crickets)	mg/mg per day	0.10	0.01	0.09	0.03	
	cal/mg	5.85	3.67	6.11	5.45	
	cal/mg per day	0.59	0.04	0.55	0.16	0.39

[a]Mg dry wt/mg dry wt animal per day
[b]Cal/mg dry wt
[c]Cal/mg dry wt animal per day
[d]Food base for the determination of the specific energy budget

to be: spring, 0.25/0.25/0.25/0.25; summer, 0.22/0.22/0.11/0.45; and fall, 0.02/0.08/0.30/0.60.

Estimates of food consumption (I), feces production (E), assimilation (A), growth (P), and respiration (R) were calculated for *Pteronemobius, Conocephalus,* and *Lycosa* (Table 9). All parameters were determined both as milligrams dry weight per milligram dry weight of animal per day and as calories per milligram dry weight of animal per day, with the exception of respiration. Assimilation was determined from

$$A = I - E, \tag{10}$$

and respiration was defined by

$$R = A - P. \tag{11}$$

Ingestion, egestion, and assimilation rates varied between the herbivores even though the production rates were identical. Ingestion, egestion, and production rates of the predator were quite different from those of the herbivores although the assimilation rates were fairly similar. Respiration rate was different for each of the species studied.

Ingestion and egestion rates for *Melanoplus* were 53% and 25% of dry body wt/day, respectively. Wiegert (1964) estimated the ingestion rate of the spittlebug *P. spurmarius,* a Homoptera-Hemiptera representative, to be 93% of dry body wt/day and the egestion rate 45%/day.

The conversion of respiratory rates (μliter O_2/mg dry wt animal per hour) for *Pteronemobius, Melanoplus, Conocephalus,* and *Lycosa* (Table 6) to energy flux (cal/mg dry wt animal per day) was 0.27, 0.18, 0.20, and 0.11 (cal/mg dry wt animal per day), respectively. The respiratory rate for spittlebugs was 0.41 cal/mg dry wt animal per day during spring (nymphs) and 0.26 during the summer and fall (adults) (Wiegert 1964). Adults of 21 species of Homoptera and Hemiptera had a mean respiratory rate of 0.17 cal/mg dry wt animal per day (Menhinick 1967). A mean value of 0.22 cal/mg dry wt animal per day was used in the present study as the respiratory rate for adult Homoptera-Hemiptera. The above respiratory rates, excluding Homoptera-Hemiptera, provide a measure of maintenance or resting metabolism. The respiration rates shown in Table 9 are total respiration values (maintenance + activity). Since these budgets were determined under one set of experimental conditions, the respiration values (R) do not show seasonal variations under different field conditions. Corrections for temperature and body size were made with equation 9. A further correction was made with the ratio of total to maintenance metabolism; this ratio (Table 6) varied from 3.57 in *Lycosa* to 1.85 for *Pteronemobius* (on litter), while *Conocephalus* (2.08) and *Melanoplus* (2.94) were intermediate. The result of equation 9 was multiplied by this ratio to obtain total metabolism for each species under field conditions.

The use of only one value (per species) for ingestion and egestion may be justified because (1) the mean seasonal temperature varied by less than 10°C in the field and (2) I and E were measured on late instar nymphs and adults which account for about 85% of the total food consumed by herbivorous insects (Waldbauer 1968).

The food consumption rates (mg/mg per day) for the arthropod species studied were converted to energy fluxes (EF_{ij} = kcal/m² per day) for field conditions by accounting for: (1) the quantity of food ingested by consumers (or predators) (p_j = per cent of dry body weight of consumer (x_j)/day); (2) the

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TABLE 10. Ecological efficiencies describing the energy flow for the adult stage of three grassland arthropod species during late summer

Species	Efficiency (%)		
	Assimilation / Ingestion	Production / Assimilation	Respiratory / Ingestion
Pteronemobius (grass)[a]	44	6	41
Pteronemobius (litter)	36	9	32
Conocephalus (grass)	38	11	29
Lycosa (crickets)	93	29	66

[a]Food base used in determination of the efficiencies.

feeding preference (w_{ij}) of the consumer; (3) the proportion that each food (or prey) component (x_i) comprised of the total available food; and (4) the calorific equivalent of the food component consumed (CE_i). The flux of energy (cal/m^2 per day) to component j from component i was then determined from

$$EF_{ij} = \frac{x_i \cdot w_{ij} \cdot p_j \cdot x_j \cdot CE_i}{\Sigma x_i \cdot w_{ij}}. \qquad (12)$$

A similar relationship was reported by O'Neill (1969), where a value p_{ij} (the probability that component j will feed on component i) was given by

$$p_{ij} = \frac{x_i \cdot w_{ij}}{\Sigma x_i \cdot w_{ij}}. \qquad (13)$$

This probability value was then multiplied by R_j (the energy loss from population j, which was assumed to be equal to the energy input in a steady state system). The value R_j is equal to the quantity ($p_j \cdot x_j \cdot CE_i$) of equation 12 which is based on the energy input to component j.

The comparison of population energy budgets must have a common basis to be meaningful. Kozlovsky (1968) has summarized the various ecological trophic efficiencies used in comparing these budgets. Three ecological efficiencies for the grassland arthropod species studied are summarized in Table 10. Assimilation efficiences reflect the amount of ingested energy that is actually utilized by the animal. Production efficiencies are an estimate of the fraction of assimilated energy which is available to be passed on to the next higher trophic level. Respiration efficiency is the fraction of ingested energy used in the metabolic processes. Assimilation, production, and respiration efficiencies were fairly similar between the herbivore species. These efficiencies at the predator level were two to three times those at the prey level, which tends to support the contention that predators replenish the relatively large quantities of energy expended in searching for and capturing prey by more efficient utilization of the energy consumed.

COMMUNITY ANALYSES

Community energetics and net production

Energetics.—In the foregoing discussions, parameters used in constructing community energy and nutrient budgets were treated individually in some detail. These parameters were also utilized in the synthesis of a model which described the flux of energy and nutrients (Na, Ca, and K) through the community and provided estimates of net primary and secondary production. Synthesis will be discussed in the energy-flow context; however, the same model is used to describe nutrient flux through the community.

Figure 7 shows the major compartments studied and their pathways of energy transfer in the grassland ecosystem. Since in a dynamic system compartments 1 through 9 will increase or decrease with time, the change in compartment size is defined as

$$\Delta C_i = \Sigma\lambda_{ij}C_i - \Sigma\lambda_{ij}C_j, \qquad (14)$$

where $\Sigma\lambda_{ij}C_i$ = total input to compartment i from all other compartments and $\Sigma\lambda_{ij}C_j$ = total loss to all other compartments. The intake rates, expressed as energy flux (cal/m^2 per day), were calculated with equation 12. The energy transferred to egestion (C_{10}) was estimated by multiplying the proportion of dry body weight egested per day times the compartment size (g m^{-2}) times the caloric equivalent (cal/g) of the compartment biomass. The respiratory energy fluxes were computed from equation 9 for each of the arthropod species except the Homoptera-Hemiptera. The major segments of the mortality compartment (C_{12}) were composed of nonpredatory mortality and predatory mortality due to causes other than *Lycosa*.

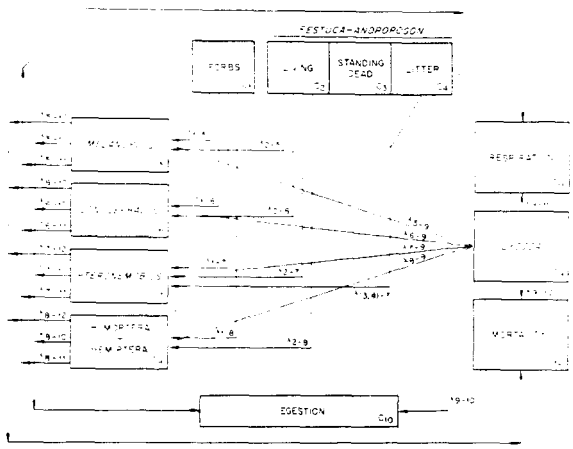

FIG. 7. A model of the grassland arthropod community showing the major compartments (C_i) and pathways of energy flux (λ_{ij}). The arrows indicate the direction of flow.

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Mortality (C_{12}) includes other components in addition to mortality; for example, cast exuviae as well as reproductive products passed on to next year's generation also are included. The actual size of this compartment was determined from

$$C_{12} = \sum_{i=5}^{9} \lambda_{i,12} C_i \,, \qquad (15)$$

where $\lambda_{i,12}C_i$ = the net flux to compartment 12 from compartment i. This flux was determined from

$$\lambda_{i,12}C_i = \sum_{j=1}^{3} \lambda_{ij}C_i - (\lambda_{i,9}C_9 + \sum_{j=10}^{11} \lambda_{ij}C_j) \,, \qquad (16)$$

where $\lambda_{ij}C_i$ = total input from compartments 1 through 3, $\lambda_{i,9}C_9$ = total loss to the predator (C_9), and $\lambda_{ij}C_j$ = losses due to excretion and respiration. The compartment (C_{12}) actually serves as a balancing component for the model. The model was evaluated weekly during the growing season (35 weeks) to provide: (1) a stepwise estimate of the energy flow through the arthropod compartments; (2) the energy fluxes among the various compartments; and (3) the net productivity of the community.

Arthropod energy flow is defined here as the respiratory energy losses plus the energy stored in tissues in each of the animal components of the community. Energy flow is then synonymous with digestive assimilation. Assimilation (= energy flow) through the primary consumer level is defined by

$$A_t = \sum_{i=5}^{8} (I_{it} - E_{it}) \,, \qquad (17)$$

where A_t = energy flow = assimilation for the herbivore trophic level at time t, I_{it} = ingestion by component i at time t, and E_{it} = egestion by component i at time t. The value A_t represents the quantity of energy (kcal/m^2 per time) which was actually utilized by the herbivore component of the community at a specific time. The total annual energy flow through the primary consumer level for the 35-week growing season was determined from

$$A = \sum_{t=1}^{35} A_t \,. \qquad (18)$$

The energy flow through the predator trophic level (C_9 = *Lycosa*) was also determined from equations 17 and 18.

Total annual energy flow through the herbivore trophic level was 60.3 kcal/m^2 (Table 11). *Melanoplus* accounted for 85.6% of this total. *Conocephalus* and Homoptera-Hemiptera contributed the remaining 14.4%; *Conocephalus* was responsible for about twice that of Homoptera-Hemiptera. The total annual energy flow through the arthropod components of the grassland ecosystem was 69.5 kcal m^2. Herbivorous species accounted for 85.3% of this total. The only omnivorous species, *Pteronemobius*, contributed 14.7%.

TABLE 11. Annual energy flow (kcal/m^2) through the dominant arthropod components of an eastern Tennessee grassland ecosystem

Herbivores			Omnivore	Predator
Melanoplus	*Conocephalus*	Homoptera + Hemiptera	*Pteronemobius*	*Lycosa*
51.6	6.0	2.7	9.2	6.1

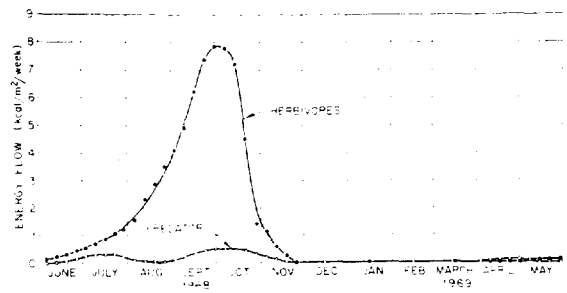

FIG. 8. Seasonal fluctuations in energy flow (kcal/m^2 per week) in the herbivore (= herbivore + omnivore) and predator trophic levels in an eastern Tennessee *Festuca* meadow.

Seasonal fluctuations in energy flow on a trophic level basis are shown in Fig. 8. The omnivore *Pteronemobius* was included in the herbivore trophic level to aid in the comparison of energy flow through the predator with that through the prey. Energy flow through the predator level expressed as a percentage of the total herbivore energy flow ranged from a maximum of 46.5% in June to a minimum of 1.3% in August, followed by a second high in November (21.5%). In the spring of 1969 the predator energy flow was as much as eight times that of the prey trophic level. These higher levels in the predator were due to the early appearance of wolf spiders in the spring (March).

The annual energy flow through the herbivore and omnivore trophic levels (69.5 kcal/m^2) was very similar to the value of 59.2 kcal/m^2 reported by Wiegert and Evans (1967) in a summary of data from an old field in South Carolina. This summary included the data of Odum et al. (1962) for three species of Orthoptera and several other insect herbivores (energy flow = 28.2 kcal m^2 per year) and the data of Golley and Gentry (1964) for the granivorous ant *Pogonomyrmex* (energy flow = 31 kcal m^2 per year). In a southern Michigan old field, herbivore energy flow was only 2.51 kcal/m^2 per year for spittlebugs (Wiegert 1964) and grasshoppers (Wiegert 1965) combined. Smalley (1959, 1960) reported 30 kcal m^2 as the annual energy flow through grasshoppers and 240 kcal/m^2 for plant hoppers in a salt marsh ecosystem. The latter value is the highest reported for an insect herbivore species. Menhinick (1967) reported a value of 4.8 kcal/m^2 per year for

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TABLE 12. Annual energy fluxes (kcal/m²) through the arthropod compartments of a grassland ecosystem

Donor compartment[a]	Recipient compartment[a]							
	C_5	C_6	C_7	C_8	C_9	C_{10}	C_{11}	C_{12}
C_1	7.83	1.56	1.76	0.67	*	*	**	**
C_2	82.60	14.74	7.81	5.22	*	*	**	**
C_3	*	*	*	*	*	*	**	**
C_4	*	*	12.64	*	*	*	**	**
C_5	*	*	*	*	3.04	38.82	24.71	23.14
C_6	*	*	*	*	1.12	10.27	5.12	1.22
C_7	*	*	*	*	1.96	12.99	6.24	1.00
C_8	*	*	*	*	0.64	3.19	1.38	−0.07
C_9	*	*	*	*	*	0.64	3.84	2.26
Total	90.43	16.30	22.21	5.89	6.76	65.91	41.29	27.69

[a]See Fig. 7
*Transfers not existing
**Transfers not pertinent to study

herbivore energy flow in a South Carolina lespedeza stand. Energy flow through the predator trophic level (6.1 kcal/m² per year) was very much greater than the annual value of 0.32 kcal/m² reported for spiders in a lespedeza stand (Menhinick 1967). Moulder (1969) reported 1.6 kcal/m² for the annual energy flow through a cryptozoan spider population in a forest community.

The annual energy fluxes among arthropod and vegetation compartments are shown in Table 12. These annual energy fluxes are represented by the $\lambda_{ij}C$ of Fig. 7. Herbivores consumed 112.62 kcal/m² per year which amounted to 8.8% of the total net primary production. *Pteronemobius*, the omnivorous species, consumed 9.57 kcal/m² per year from green vegetation and 12.64 kcal/m² per year from detritus (standing + litter). The ingestion of approximately 9% of net primary production was higher than values reported in other studies. Smalley (1960) estimated that the grasshopper *Orchelimum* consumed about 2% of annual net production by salt marsh grass. Wiegert and Evans (1967) reported that less than 1% of annual net primary production was consumed by grasshoppers and spittlebugs. They further concluded that adding the other consumer groups would increase the estimate to only 5%. Insect herbivores feeding on lespedeza ingested 0.9% of annual net primary production (Menhinick 1967). Reichle and Crossley (1967) estimated vegetation consumption by insect herbivores to be about 5% of the foliage standing crop in a forest community. The value reported in the present study for vegetation consumption by insect herbivores probably reflects a very large proportion of the total in that grassland.

Annual input to the predator compartment (*Lycosa* = C_9) in the form of ingested prey species was 6.76 kcal/m². *Melanoplus* contributed 45% of this amount. *Conocephalus* and *Pteronemobius* accounted for 17% and 29%, respectively. The Homoptera-Hemiptera were responsible for the remaining 9%. Although the total ingestion values represent a reasonably good estimate of annual food consumption by wolf spiders, the individual values are biased upward since they were the only prey species considered. It is almost certain that wolf spiders encounter other prey species upon which they will readily feed (e.g., Lepidoptera and Coleoptera larvae, etc.). These prey species appeared only occasionally in the weekly biomass samples. Also, *Lycosa* are cannibalistic.

The total flux to compartment 10 (egestion) was 65.91 kcal/m², which accounted for 47% of total input to the arthropod component of the community. Respiratory energy flux totaled 41.29 kcal/m² per year for the arthropod species studied. This represented almost 29% of the total arthropod ingestion. Mortality (as determined by equation 15) for the prey species was 32.05 kcal/m² per year, which represented the actual loss of protoplasm from this trophic level. Included in this total were nonpredatory and predatory mortality, cast exuviae, and reproductive products. Egg production in some instances would not be considered as a loss. However, in prey species that have but one generation per year, reproduction products represented the production that was removed from the active portion of the community until the following season. Predation by wolf spiders (6.76 kcal/m² per year) accounted for 21.1% of the total prey mortality, which constitutes a significant contribution by *Lycosa* to the total herbivore-omnivore mortality. The absence of other invertebrate predators in the community indicates that *Lycosa* was the dominant invertebrate predator. Moulder (1969) found that, during spring and summer, spiders in a forest-floor community accounted for daily equivalents of 1.2% and 0.9% of the prey biomass, respectively. Predation pressure then dropped to 0.4% during the fall and winter. Numerous other predator species (e.g., centipedes and pre-

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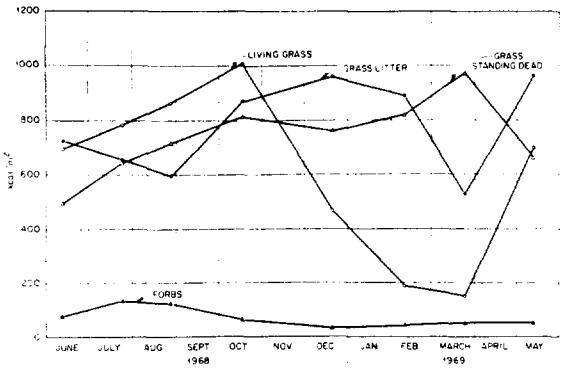

FIG. 9. Standing crop energy (kcal/m²) of the four components of vegetation in an eastern Tennessee grassland ecosystem. Points shown are based on means of 12 biomass determinations at each sampling period and on means of three caloric determinations on the pooled biomass sample.

dacious beetles) which competed with the spiders existed in this cryptozoan community.

Net primary production.—The standing crop energy (kcal/m²) for the vegetational components was determined from the data of Tables 3 and 4 and Fig. 1 and 2 (Fig. 9). There were no significant seasonal differences ($P \leq 0.05$) between the standing dead grass and litter. The living portion of the grass differed from the dead components and from forbs ($P \leq 0.05$). The living grass was the only vegetational component which differed ($P \leq 0.05$) in total energy content (kcal/m²) through time.

The problems associated with determining net primary production have been discussed in some detail by Wiegert and Evans (1964). Of major concern are: (1) the occurrence of peak standing crops of different species at different times during the growing season; (2) green plant mortality before the maximum standing crop is realized; and (3) the consumption of vegetation by insects. These factors which affect the estimation of net primary production are considered in the following discussion.

The peak standing crop of *Festuca* and *Andropogon* occurred simultaneously in October at 716.9 and 292.1 kcal/m², respectively. *Festuca* and *Andropogon* exhibit premaximal standing crop mortality at rates of 12.9 and 1.4 kcal/m² per year, respectively (Kelly et al. 1969). Adjustment of each standing crop for this mortality resulted in values of 729.8 kcal/m² for *Festuca* and 293.5 kcal/m² for *Andropogon*. Since no data were available on forb mortality, the observed standing crop (128.6 kcal/m²) was not corrected. The consumption of green vegetation by herbivores and omnivores amounted to 9.7% of the grass (110.37 kcal/m² per year) and 8.4% of the mixed green forbs (11.8 kcal/m² per year). Incorporation of these values resulted in an annual net production of 1,133.7 kcal/m² by the grasses (*Festuca* + *Andropogon*) and 140.4 kcal/m² by the green forbs. The net result totaled 1,274.1 kcal/m², which was the net primary production by the grassland community. A value of 4,400 kcal/m² was reported for this same community for the 1967 growing season (Kelly et al. 1969). However, precipitation during the 1967 season was four times that of the 1968–69 season and three times greater than the 30-year mean. In an upland area of needlegrass and Canada bluegrass and about 10 species of green forbs in southern Michigan, Wiegert and Evans (1964) reported the net primary production to be 1,328 kcal/m² for 1959 and 1,392 kcal/m² for 1960.

Net secondary and tertiary production.—Secondary production has been defined as the calorific equivalent of the protoplasm produced in the secondary trophic level (Wiegert and Evans 1967). In this context net secondary production is given by

$$NP_s = A - R\,, \tag{19}$$

where NP_s = net secondary production, A = assimilation, and R = respiration. Secondary production is most accurately determined from information on standing crop (biomass) and the instantaneous growth rate of the species for the time period under consideration (Wiegert 1965). However, growth rates are generally not constant throughout the growing season. For this reason Wiegert chose to calculate net secondary production as

$$NP_s = S + \sum_{i=2}^{n} \left[\frac{(N_i + N_{i-1})}{2} \cdot (W_i - W_{i-1}) \right] \tag{20}$$

where S = standing crop at time $i = 1$, N_i = number of animals per square meter at time i, and W_i = mean weight per animal at time i. Equation 20 does not account for production which is removed from the arthropod compartment during the growing season. These unaccounted-for variables are considered in the equation

$$NP_{s,t} = \sum_{i=5}^{8} [\lambda_{i,9,t} C_{9,t} + \lambda_{i,12,t} C_{12,t}]\,, \tag{21}$$

where $NP_{s,t}$ = net secondary production (kcal/m²) at time t, $\lambda_{i,9,t} C_{9,t}$ = flux from herbivores and omnivore (C_i) to the predator (C_9) at time t, and $\lambda_{i,12,t} C_{12,t}$ = flux from the herbivore and omnivore compartments to the mortality compartment (C_{12}) at time t (see previous discussion on C_{12}). Annual net secondary production may then be determined from

$$NP_s = \sum_{t=1}^{35} NP_{s,t}\,, \tag{22}$$

where 35 weeks is the length of the growing season. Production by the spider component of the arthropod community (tertiary production) was determined in the same way as secondary production with the omission of the first term of equation 21. It should

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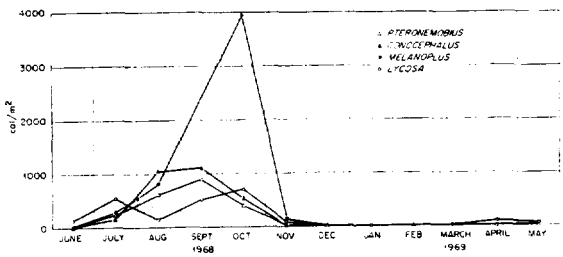

FIG. 10. Energy content (cal/m²) of the arthropod component of a grassland ecosystem in eastern Tennessee. Points shown are based on 32 biomass determinations at each sampling period and on means of two caloric determinations on the pooled biomass samples.

be pointed out that the present equation (21) as well as that of Wiegert (20) can be negative when the mean weight per animal decreases during the growing season. Negative net production (secondary and/or tertiary) can be possible during certain stages of the developmental period (e.g., egg laying).

Energy content (cal/m²) for four of the arthropod species studied is shown in Fig. 10. The Homoptera-Hemiptera were not included because of low values obtained for these groups. When a mean caloric content of 5,027 cal/g dry wt was used for these two orders, the standing crop energy (cal/m²) of the Homoptera-Hemiptera compartment was calculated to be: June, 77.1; July, 120.3; August, 40.2; September, 15.0; and October, 75.4. The energy content of this compartment then declined to zero until the following spring when the level rose to 49.0 cal/m² in May and 71.4 in June.

No differences occurred between the standing crops of *Pteronemobius* and *Conocephalus*. Both, however, had higher energy standing crops than the Homoptera-Hemiptera compartment when compared over the entire growing season. The standing crop energy of *Melanoplus* was much higher than any of the other herbivore species.

Annual net secondary production was determined from equations 21 and 22 as: *Melanoplus*, 26.18 kcal/m²; *Conocephalus*, 2.34 kcal/m²; *Pteronemobius*, 2.96 kcal/m²; and Homoptera-Hemiptera, 0.57 kcal/m². Total net tertiary production by *Lycosa* was 2.26 kcal/m². *Melanoplus* accounted for 82% of the total net secondary production. *Conocephalus* and *Pteronemobius* contributed 7% and 9%, respectively. The Homoptera-Hemiptera produced only 2% of the total. The total net production by the arthropod component (secondary + tertiary) was 34.31 kcal/m² of which the predator constituted 6.6%.

The value reported here for total net productivity (34.31 kcal/m² per year) is higher than most of the values reported in the literature for comparable arthropods in grassland habitats. Odum et al. (1962) found that *Melanoplus* was the dominant herbivore in the early successional stages of old field development. They reported a productivity of 4.5 kcal/m² per year for the herbivore component of the community. In a 30-year-old field in southern Michigan, Wiegert (1964, 1965) found net secondary production by insects to be 0.69 kcal/m². Smalley (1959, 1960) reported a value of 81 kcal/m² for annual net secondary production by both grasshoppers and plant hoppers: the latter constituted 86% of the total. Production in this case occurred on a monophytic stand of *Spartina*, a highly productive salt marsh grass. The relatively high values reported in the present study as well as some previously reported values were probably due to higher primary productivity by the vegetational component of the community or by greater accuracy in determining secondary production due to the refinement of productivity equations.

Annual energy budget.—An annual budget for energy flow and net production by the arthropod and vegetational components of the grassland ecosystem is shown in Fig. 11. The values inside the compartments indicate the total net primary, secondary, or tertiary production (kcal/m²) for the 1968–69 growing season. The arrows indicate the direction of energy fluxes. Values over the arrows represent annual energy fluxes ($\lambda_{ij}C$ of Fig. 7) determined from the data of Table 12. Consumption of vegetation was the only output considered for primary producers in constructing the budget. Secondary production was partitioned between predatory and nonpredatory mortality because the standing crop for this compartment eventually approaches zero in the system. The relative amounts of energy flowing between the various compartments have been previously discussed. In the present discussion these values along with production data were used to calculate the ecological effi-

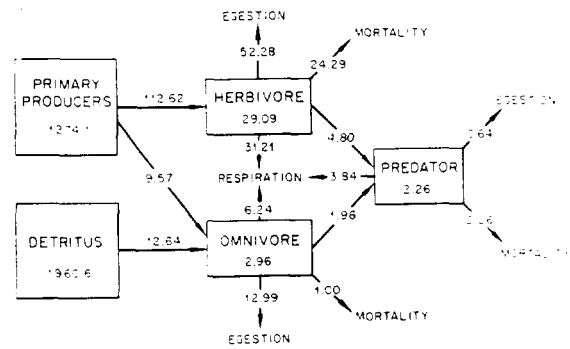

FIG. 11. Annual energy budget of energy fluxes and net production (kcal/m²) by the arthropod and vegetation components of an eastern Tennessee grassland ecosystem. The values inside compartments represent net production (exception: for detritus value equals standing crop of standing dead and litter), and the values on arrows represent energy fluxes. Arrows indicate the direction of flow.

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TABLE 13. Trophic level comparisons of energy flow and net production for the arthropod and vegetational components of a grassland ecosystem (the subscripts n and $n-1$ denote the respective trophic levels)

Trophic level	Ecological efficiency ratios[a]								
	$\frac{A_n}{I_n}$[b]	$\frac{R_n}{I_n}$	$\frac{P_n}{I_n}$	$\frac{NP_n}{I_n}$	$\frac{I_n}{I_{n-1}}$	$\frac{A_n}{A_{n-1}}$	$\frac{R_n}{R_{n-1}}$	$\frac{I_n}{NP_{n-1}}$	$\frac{NP_n}{R_n}$
Herbivore	.54	.28	.04	.26	—[d]	—	—	.09	.93
Omnivore	.41	.28	.09	.13	—	—	—	.01	.47
Range from literature[c]	.30–.80	.23–.32	.08–.27	.05–.75	—	—	—	.01–.06	.19–.06
Predator	.90	.57	—	.33	.05	.09	.10	.21	.59
Range from literature[c]	.90–.98	.52–.67	—	.32–.38	.09–.18	.07–.18	.05–.25	.12–.33	.39

[a]Ratios explained in text.
[b]A = assimilation; I = ingestion; R = respiration; P = production passed on to next higher trophic level; and NP = net production.
[c]Ranges obtained from summary of Kozlovsky (1968) and from data of Smalley (1959, 1960), Engelmann (1961), Odum et al. (1962), Wiegert (1964, 1965), Reichle and Crossley (1967), Menhinick (1967), and Moulder (1969).
[d]Ratios not applicable.

ciency ratios (Table 13). The definitions of each of these ratios with the exception of NP_n/R_n are after Kozlovsky (1968). The ratio NP_n/R_n was taken from Wiegert (1965). The ratios are defined as follows:

Assimilation efficiency	(A_n/I_n)	= ratio of assimilated energy to ingested energy
Respiration efficiency	(R_n/I_n)	= ratio of energy expended in metabolism to ingested energy
Ecological efficiency	(P_n/I_n)	= ratio of energy passed on to the next higher trophic level to the ingested energy
Ecological growth efficiency	(NP_n/I_n)	= ratio of the total energy available to be passed on to the next higher trophic level to the ingested energy
Transfer efficiency	(I_n/I_{n-1})	= ratio of energy ingested in trophic level n to that ingested in trophic level $n-1$
Progressive efficiency	(A_n/A_{n-1})	= ratio of energy assimilated in trophic level n to that assimilated in trophic level $n-1$
Respiratory ratio	(R_n/R_{n-1})	= ratio of energy used in metabolism in trophic level n to that used in trophic level $n-1$
Consumption efficiency	(I_n/NP_{n-1})	= ratio of energy ingested by consumers to the net production by the preceding trophic level
Secondary $\frac{\text{production}}{\text{respiration}}$	(NP_n/R_n)	= ratio of energy accumulated to the energy expended in metabolism

The efficiencies reported in Table 13 are in good agreement with those reported in the literature with three exceptions. First, the low P_n/I_n value reported for herbivores (0.04) resulted from the following: (1) only one predator genus was considered and (2) the dominant herbivore (*Melanoplus*) was the least "catchable" species. These resulted in reduced numbers of prey being consumed. Secondly, the ratio of ingestion by herbivores to net primary production (I_n/NP_{n-1}) was higher than any of the literature values probably because of the relatively larger herbivore biomass found in this study. Thirdly, the ratio of net production to respiration (NP_n/R_n) for herbivores was much higher than any value found in the literature. This may result from the high productivity of this community and the underestimated respiratory energy losses. For predators, the only comparable value was one found for a forest-floor community (Moulder 1969) where the productivity was low compared to the grassland studied here.

The results presented in Table 13 lend additional support to two hypotheses concerning trophic dynamics of ecological systems. First, Slobodkin (1960) suggested that food-chain efficiencies fall in the range of 6% to 15%. In the present study, values of I, A, and R were 5–10% of the respective values in the next lower trophic level. Secondly, Lindeman (1942) stated that consumers at progressively higher positions in a food web utilize their food supply at progressively higher efficiencies. The results of the trophic efficiency ratios A_n/I_n, R_n/I_n, NP_n/I_n, and I_n/NP_{n-1} tend to support this contention that transfer efficiencies are higher at higher trophic levels.

Community nutrient fluxes

The fluxes of sodium, calcium, and potassium among the arthropod and vegetational compartments were determined utilizing the community model developed earlier (see Fig 7). In determining the nutrient fluxes, two major changes were incorporated within the model: (1) the respiration compartment was removed and (2) equation 7 was included to estimate the nutrient concentrations in arthropod feces. The nutrient concentrations in the various compartments (Tables 3 and 5) were used in the

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TABLE 14. Annual (April through November) fluxes of sodium, calcium, and potassium (mg/m²) through the arthropod compartments of a grassland ecosystem

Donor compartment[a]	Recipient compartment[a]							
	C_5	C_6	C_7	C_8	C_9	C_{10}	C_{11}	C_{12}
Sodium								
C_1	0.42	0.09	0.09	0.05	*	*	**	**
C_2	21.38	3.46	1.77	1.04	*	*	**	**
C_3	*	*	1.07	*	*	*	**	**
C_4	*	*		*	*	*	**	**
C_5	*	*	*	*	0.41	1.87	*	19.52
C_6	*	*	*	*	0.15	0.64	*	2.76
C_7	*	*	*	*	0.40	0.72	*	1.81
C_8	*	*	*	*	0.21	b	*	0.88
C_9	*	*	*	*	*	0.41	*	0.76
Total	21.80	3.55	2.93	1.09	1.17	3.64	*	25.73
Calcium								
C_1	17.10	3.43	3.76	1.46	*	*	**	**
C_2	44.86	8.03	4.26	2.94	*	*	**	**
C_3	*	*	14.35	*	*	*	**	**
C_4	*	*		*	*	*	**	**
C_5	*	*	*	*	0.43	54.30	*	7.23
C_6	*	*	*	*	0.08	10.71	*	0.67
C_7	*	*	*	*	0.36	12.17	*	9.94
C_8	*	*	*	*	0.13	b	*	4.27
C_9	*	*	*	*	*	0.65	*	0.35
Total	61.96	11.46	22.47	4.40	1.00	77.83	*	22.46
Potassium								
C_1	4.55	1.12	1.36	0.85	*	*	**	**
C_2	47.76	13.41	7.11	6.42	*	*	**	**
C_3	*	*	10.79	*	*	*	**	**
C_4	*	*		*	*	*	**	**
C_5	*	*	*	*	0.45	2.69	**	49.17
C_6	*	*	*	*	0.08	0.44	*	14.01
C_7	*	*	*	*	0.47	5.36	*	13.43
C_8	*	*	*	*	0.42	b	*	6.85
C_9	*	*	*	*	*	0.55	*	0.87
Total	52.31	14.53	19.26	7.27	1.42	9.04	*	84.33

[a]See Fig. 7
[b]No data available
*Transfers not existing
**Transfers not pertinent to study

model to develop an annual budget for each of these three elements in the grassland ecosystem (Table 14 and Fig. 12). The values inside the compartments (Fig. 12) indicate the standing crop of nutrients (mg/m²). Values over the arrows represent annual nutrient fluxes ($\lambda_{ij}C$ of Fig. 7) determined from the data of Table 14.

Total trophic level intake of sodium by herbivores was 26.4 mg/m² per year, and by omnivores, 2.9 mg/m² per year. The herbivores egested only 9.5% (2.5 mg/m² per year) of the total annual intake of sodium, which resulted in a utilization of about 90% of ingested sodium. This is consistent with the results presented earlier, where the herbivores also concentrated (retained) sodium on a per gram basis. A small error (about 2%) was involved in that no elimination data were available for the few Hemoptera-Hemiptera species. The omnivore *Pteronemobius* retained 59% of annual sodium intake, which suggests that it too conserved sodium.

Calcium and potassium intake were similar for each trophic level. Herbivores ingested 77.8 mg/m² per year of calcium and 74.1 mg/m² per year of potassium. *Pteronemobius* ingested 22.5 mg/m² per year of calcium and 19.3 mg/m² per year of potassium. The similarity within trophic levels did not hold when calcium and potassium egestion were considered. Herbivores egested 83% of ingested calcium and

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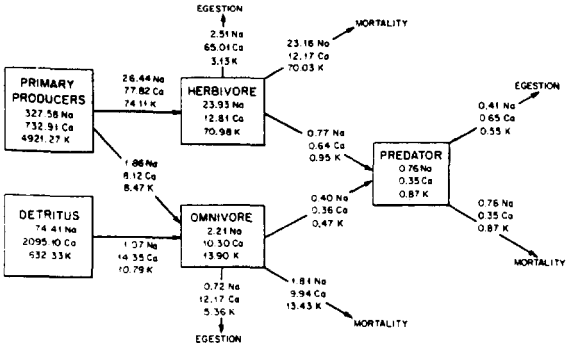

FIG. 12. Annual nutrient budget (mg/m^2) for sodium, calcium, and potassium showing the maximum standing crops of nutrient (values inside compartments) and nutrient fluxes (values on arrows) through the arthropod and vegetation components of an eastern Tennessee grassland ecosystem. Arrows indicate direction of flow.

only 4% of ingested potassium, indicating that the requirements for these elements were different—17% utilization of calcium and 96% utilization of potassium. The high rate of calcium turnover was due to the large proportion of ingested calcium which was not assimilated by *Melanoplus* (see Table 2). The omnivore *Pteronemobius* egested 54% of ingested calcium and 28% of ingested potassium. The difference in turnover of these two elements in the omnivore trophic level was not as extreme as in the herbivore trophic level, but was a twofold increase in potassium utilization over that of calcium. The difference in the turnover of these two elements was due to relatively large amounts of unassimilated calcium passing directly through the population.

Trophic level intake of sodium, calcium, and potassium by spiders (*Lycosa*) was similar in all respects. These ingestion values represented 4.6% of the total sodium removed from the prey population via mortality, 4.3% of the total calcium, and 1.7% of the total potassium. Egestion of these three nutrients was different; 35% of ingested sodium, 65% of ingested calcium, and 39% of ingested potassium were egested. None of these three nutrients appears to be retained to any great extent in the predator trophic level.

If the components of an animal community have no physiological requirements for a nutrient present in the food source, the concentration of this nutrient should not be expected to change with higher trophic position in the food chain. If, on the other hand, there is a physiological requirement for this nutrient by the community and the nutrient is present in limited quantities in the food base, then this nutrient should be concentrated by primary consumers. This was found in the present study where primary consumers (herbivores and omnivores) concentrated sodium, but not potassium or calcium, above the levels

TABLE 15. Trophic level comparisons of nutrient fluxes through arthropod and vegetation components of a grassland ecosystem (the subscripts n and $n-1$ denote the respective trophic levels)

Trophic level	Ecological efficiency ratios[a]				
	$\frac{{}^{b}A_n}{I_n}$	$\frac{P_n}{I_n}$	$\frac{I_n}{I_{n-1}}$	$\frac{A_n}{A_{n-1}}$	$\frac{I_n}{NP_{n-1}}$
			Sodium		
Herbivore	.91	.03	—[c]	—	.08
Omnivore	.75	.14	—	—	.01
Predator	.65	—	.04	.03	.05
			Calcium		
Herbivore	.16	.01	—	—	.11
Omnivore	.46	.02	—	—	.01
Predator	.35	—	.01	.02	.04
			Potassium		
Herbivore	.95	.01	—	—	.02
Omnivore	.72	.02	—	—	.01
Predator	.61	—	.02	.01	.02

[a]Ratios explained in text.
[b]A = assimilation; I = ingestion; P = production passed on to the next higher trophic level; and NP = net production.
[c]Ratios not applicable.

found in vegetation, whereas predators did not concentrate any of these elements significantly above the levels in prey. The low retention of calcium by both prey and predator trophic levels suggests that calcium is required in smaller quantities in arthropod physiological processes than are sodium and potassium (see Roeder 1953). Potassium concentrations were apparently high enough in vegetation to require no further concentration by the primary consumers. Reichle et al. (1969) also reported a concentrating of nutrient elements in the early links of a forest-floor arthropod food chain. Saprovores (prey) concentrated sodium and potassium, but not calcium (with the exception of millipedes), whereas the predators (spiders, beetles, etc.) concentrated none of these elements above the levels in prey. Apparently primary consumers, the first link in the food chain, accumulate required nutrients to a far greater extent than do secondary and tertiary consumers. This is to be expected, since the secondary and tertiary consumers require the essential nutrient in approximately the same concentrations as do the primary consumers.

Trophic level comparisons of nutrient fluxes through the arthropod and vegetational components of the grassland studied are shown in Table 15. Although the ratios presented have been used only for energetics data, they also provide a means for comparing the distribution of sodium, calcium, and potassium among the three trophic levels studied.

Assimilation efficiencies (A_n/I_n), reflecting the fraction of ingested nutrient incorporated into the

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biomass and utilized by the trophic level, were very similar for sodium and potassium within each trophic level. Trophic level incorporation of calcium was different from that of sodium and potassium: a smaller fraction of ingested calcium was utilized by each of the trophic levels. Ecological efficiencies (P_n/I_n) express the fraction of ingested nutrient which is actually passed on to the next higher trophic level via predation. These ratios were quite similar for each of the nutrients studied here with one exception. The P_n/I_n ratio for sodium in the omnivore was almost seven times the value of this ratio for sodium in herbivores. This undoubtedly is due to the very low concentration of sodium in the detritus food base (0.19 mg/g AFDW).

The efficiency ratios shown in Table 15 also are useful for describing nutrient transfer between trophic levels and nutrient redistribution within recipient trophic levels. Trophic level transfer ratios (I_n/I_{n-1}) and progressive assimilation efficiencies (A_n/A_{n-1}) were similar for each of the three elements studied. These ratios ranged from 10% to 20% of their respective energy values (Table 13), indicating that energy flowing through the ecosystem is retained less efficiently than are nutrients. These lower energy-retention efficiencies reflect the fact that energy flows freely through successive trophic positions in the food chain from an ordered available state to a state of disorder and unavailability (Phillipson 1966). Nutrients, on the other hand, are retained by organisms in food chains to be utilized and then recycled within the organism for further use.

Consumption efficiencies (I_n/NP_{n-1}) depicting the transfer of nutrient elements between trophic levels, i.e., nutrients incorporated in primary production to consumers, varied considerably among trophic levels, but were fairly similar within omnivore and predator trophic levels for the elements studied. The herbivore trophic level was an exception. The low value obtained for the ratio of potassium ingested by herbivores to that incorporated in net primary production was due to the high levels of this element in living vegetation (14.3 mg K/g AFDW) as compared to the levels in herbivores (1.9 mg K/g AFDW). The ratio for the omnivorous species (1.3 mg K/g AFDW), although still based on plant material, was not affected here because more than 50% of the potassium input was obtained from the detritus food base which was relatively low in potassium (2.5 mg K/g AFDW).

The preceding results suggest that sodium and potassium behave similarly in their movement through arthropod food chains. Both nutrients were present at approximately twice the concentration of calcium (mg/g AFDW) in the two major arthropod trophic levels. Sodium-to-potassium ratios for the prey and predator trophic levels were 0.63 and 0.98, respectively. High levels of potassium in vegetation (14.3 mg/g AFDW) were responsible for the lower Na:K ratio obtained for prey. Roeder (1953) has shown that arthropods have similar physiological requirements for sodium and potassium. This similarity should be applicable to entire trophic levels. The low concentrations of calcium in the two major trophic levels and the rapid elimination of this element from each trophic level indicate that calcium is not required in as large a quantity as are sodium and potassium in this arthropod community.

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